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Edward Salisbury

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THE PIONEER VEGETATION OF EXPOSED MUDS AND ITS BIOLOGICAL FEATURES

By SIR EDWARD SALISBURY, F.R.S.
'Croindene' Strandway, Felpham, Sussex

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CONTENTS

The characteristic pioneer flora of exposed mud in Britain, here considered, is held to comprise about fifty species, most of which are local in their occurrence, often conspicuously intermittent, and very variable in their abundance. The majority are annuals whilst others, potentially perennial, may behave as annuals. Their provenance is prevailingly Southern or Continental.

The fruiting periods exhibit a marked late-summer or autumnal bias corresponding with the season of greatest evaporation and frequency of suitable habitat conditions. Most of the 'mud-species' have greatly diminished in their frequency, the average loss being probably about 40% of their former locations. The importance of recording their biological characteristics in Britain, before they become extinct, is emphasized. The propagules are shown to be generally small, or very small, with transport by adhesion to the feet and feathers of water-birds as probably the most frequent means of more distant dispersal, although internal carriage may be effective for some species over long distances.

Estimates respecting the average and observed maximum outputs for 36 species are furnished and, as with other 'intermittently available habitats', these are shown to be very large especially in relation to the size of most of the plants.

The mode of germination is illustrated by data from experimental sowings, of freshly ripened propagules, of 38 of these species. The germination behaviour, it is shown, may vary conspicuously as between the different species, sometimes even between individuals of the same taxon, but there is a prevailing tendency, especially marked with some species, towards quasi-simultaneous germination of the seeds or fruits maturing at the same time. Germination experiments, involving large numbers of seeds or fruits from different individuals, have shown that while, frequently, there may be no germination in darkness, the propagules from certain individuals of the same species may yield a small or moderate percentage in the dark. The response to light is probably a matter of degree rather than of kind. Whilst the average behaviour, in this and other respects, is of great significance it is emphasized that the diversity of biological characteristics, which experimental cultures reveal, *in the offspring of different individuals* (termed 'polybiosis') may be of great importance for the exploitation of abnormal circumstances and perhaps even for survival. Most 'mud-species' have very small propagules and either exhibit no germination in darkness or a very low percentage. The small number of species with relatively large propagules yield appreciable germinations in the dark. These 'mud-species' exhibit, in varying degrees, significant specialization for the colonization of bare mud and are intolerant of competition.

Cogent evidence is furnished that emphasizes the importance, for experiments on wild species, of utilizing propagules derived from a single individual to permit of valid conclusions as to the effect of contrasting conditions.

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INTRODUCTION

The interesting and specialized flora of exposed mud is, as the sequel will indicate, disappearing rapidly. So it is obvious that the opportunities for its study may soon be lost: hence it is important that such data as are available concerning its features should be placed on record.

For the present purpose the term 'mud' is held to imply a previously inundated soil surface, irrespective of whether this is prevailingly argillaceous, sandy, or peaty. Where such muds border the larger, more permanent, areas of inundation a gradual lowering of the water-table may only enhance the vigour and centrifugally extend the zone of the 'reed-swamp' species, or other shallow-water vegetation, so that, normally, a severe summer drought (or artificially abrupt lowering of the water-level in a lake or reservoir) will alone provide an expanse of bare mud where pioneer species can colonize and flourish. In the smaller ponds and shallower depressions subject to winter inundation, however, the desiccation in most summers may provide a sufficient check to the vigour, or even prevent survival, of perennial species, at least marginally, and this repression may be markedly reinforced, in the more severe winters, by the phenomenon of 'frost-lifting' with benefit to those species which germinate entirely (e.g. *Polygonum minus*) or mainly in the spring (e.g. *Anagallis minima*, *Lythrum hyssopifolia*). In these pools, consequently, exposed mud is also provided that permits colonization by, and persistence of, short-lived species that, by virtue of seed dormancy, can evade the lethal effects of the environmental vicissitudes.

The account which follows presents data which would appear to establish that the species concerned are not an accidental assemblage but represent a community of associated types that share a number of specialized features favourable to meet the peculiarities of this intermittently available habitat. The number of these species to be found growing together, on a high proportion of exposed muds, is small. Such include *Juncus bufonius* and *Gnaphalium uliginosum*. But though the frequency of these is high their abundance, like that of other 'mud-species', is conspicuously variable.

The great majority of the species characteristic of exposed muds are actually of local, sometimes extremely local, occurrence, which suggests their need for an infrequent combination of environmental conditions. Such localization does, however, add significance to the fact that, though only a small proportion of the rarer species may be found in a single locality in the same season, the various combinations of such species that have been found growing together, in one locality or another, collectively embrace the entire range of those listed in table 1. A few instances will suffice to illustrate this feature.

On Colney Heath, in Hertfordshire, nineteen of the species listed have occurred and, apart from the more widespread types, included: the two species of *Bidens*, *Damasonium alisma*, *Lythrum hyssopifolia*, *Polygonum minus*, *Pulicaria vulgaris*, *Radiola linoides*, *Ranunculus hederaceus*, *R. omiophyllus*, *Rorippa islandica*, *Veronica anagallis-aquatica*, and *Veronica scutellata* var. *villosa*. On the mud of the Brent Reservoir in Middlesex, local species that in some years have been abundant are *Chenopodium rubrum*, *Rorippa islandica* and *Rumex palustris* with *Alopecurus aequalis* frequent, *Myosoton aquaticum* occasional and *Limosella aquatica* rare. The sandy and peaty mud of Shalford common in Surrey once yielded, *inter alia*, *Cyperus fuscus* in quantity, also *Limosella aquatica* and *Pulicaria vulgaris*. The shallow pools at the Lizard have provided *Anagallis minima*, *Cicendia filiformis*, and *Radiola linoides* together with *Juncus capitatus* and *J. mutabilis*. Except for the dwarf rushes, a similar association of species has been seen on the Dorset heaths with the addition of *Crassula tillaea*.

The more characteristic 'mud-species' are enumerated in table 1 and lists have been prepared of those which occur, or were formerly to be found, in thirty-one localities distributed through 12 of the southern English counties. In any single habitat the number was found to vary from 20 species to as few as four, with an average of nine. The muds these species colonize are usually well supplied with organic material, the more argillaceous muds often least so, whilst the siliceous muds may be rich in humus and even peaty. Both types are mostly very fertile and tend to have a teeming population of micro-organisms so that, compared with the air generally, the atmosphere above the muds may be expected to exhibit a marked enrichment of CO_2 and a diminution of oxygen. Both the higher proportion of CO_2 and the diminished oxygen, as recently shown by Bjorkman, can promote a marked acceleration of photosynthesis. The foregoing features then, as also the dark colour of many exposed muds, which in sunshine consequently attain to higher temperatures, all promote a vigorous growth of the colonizing plants. As illustrating this feature, one may cite the growth of *Riccia crystallina*, which often follows the alga, *Botrydium granulosum*, as a pioneer colonizer of exposed muds. The hepatic forms rosette-like plants which, according to MacVicar (1912, p. 26), range in diameter from 11 to 22 mm. However, on the blackish mud of a dried up pool, most of the plants greatly exceeded that maximum and a number were measured that were over 40 mm in diameter! The exceptionally large growths, that can be attained on organically rich mud by plants of *Bidens cernua* (150 cm), of *Chenopodium rubrum* (200 cm), of *Ranunculus sceleratus* (120 cm) and of *Rumex palustris* (120 cm), further exemplify this propensity.

A natural consequence of this high fertility is a correspondingly augmented severity of the competition pressure and a probable acceleration of the successional changes. Thus were it not for the periodic and catastrophic transformation from exposed and desiccating mud to complete, and sometimes prolonged, submergence, the more characteristic annual species could be permanently eliminated.

The occurrence of many of these annual 'mud-species' in habitats that are inundated in winter has been the subject of comment by a number of experienced field-botanists. This feature might suggest that frost as well as inundation plays a significant role in their localization. However, the fact that two of the species particularly characteristic of situations subject to winter inundation, namely *Myosurus minimus* and *Cicendia filiformis*, both extend their range into the Mediterranean region and the former into California and North Africa, would seem to indicate that low-temperature submergence is not essential.

Moreover, individuals of both these species, as well as of *Limosella aquatica*, *Lythrum hyssopifolia* and *Polygonum minus* have produced self-sown offspring and flourished, although grown in pots and not subjected to winter inundation. This suggests that the winter submergence, as well as the summer desiccation, may have their main significance as diminishing the competitive pressure from other species, rather than as conferring a direct benefit.

Both *Cicendia* and *Myosurus* illustrate the very marked localization already referred to. *Myosurus minimus*, as White (1912, p. 144) has recorded and, as has been noted elsewhere, may be restricted to different parts of a particular field in successive years. *Cicendia filiformis* has been seen in certain depressions, year after year, sometimes in abundance, yet, even then, absent from apparently similar depressions nearby. The easy dispersal of the propagules of both these species by wind renders extreme localization the more significant.

The experiments carried out by Guppy (1912, p. 480) clearly demonstrated that both *Bidens cernua* and *B. tripartita* can survive conditions of appreciable drought and yet produce viable fruits. At the other extreme these species frequently grow in shallow water. Similarly, *Chenopodium rubrum* has been encountered growing in moist organic mud where it can attain a height of 200 cm but is also to be found growing in abundance on almost dry mud, to a height of scarcely a centimetre but fruiting freely (figure 9*E*). These and other pioneer annuals that colonize the exposed mud may obviously be subjected to a wide range of conditions, from a very dilute soil solution, following heavy rainfall, to a high concentration when rainfall is absent and conditions of high evaporation have obtained. It is therefore relevant to note that Gurlitt (1918, p. 273) grew *C. rubrum* successfully in culture solutions of widely differing concentrations, and the resulting plants exhibited osmotic pressures of their cell-saps ranging from 13 to 64 atmospheres. Such facts sufficiently attest the remarkable adaptability of the members of the 'mud-flora' and this enables them to meet the rapidly fluctuating vicissitudes of their environment. It may be noted that, in the north, Hanson & Pedersen (1968, p. 266) regard *C. rubrum* as indigenous to salt marshes and muddy saline erosion hollows. Williams (1969) assesses *C. rubrum* as indifferent to soil reaction but requiring a high nitrate supply. Since his account is mainly concerned with the ecotypes which are associated with artificial habitats, the applicability of his generalizations to the plants of the mud flora may not be valid.

A similar tolerance for soils rich in ions is no doubt responsible for the prevalence of *Rumex maritimus* and *Samolus valerandi* in coastal areas, whilst *Chenopodium rubrum*, *Limosella aquatica*, *Lythrum hyssopifolium* and *Ranunculus sceleratus* have all been found flourishing on salt-marsh soils. It is to be noted that both *Rumex maritimus* and *Samolus valerandi* appear to have diminished far more conspicuously from their inland stations. The latter species, for instance, is recorded by Forster (1816, p. 31) as 'formerly in great abundance' near Tunbridge Wells.

In the older writings, when these 'Mud species' were far more prevalent, their occurrence 'where water has stagnated during winter' is repeatedly emphasized and this stresses their association with poorly-drained soils. Such soils, as A. B. Stewart has pointed out (1965), have a higher content of most trace elements, attributable to their increased mobilization and the more available since they are often chelated. These edaphic factors may influence the striking localization.

Even in habitats that, from their origin, tend to be deficient in bases the alluvia are ameliorated by solutes leached from the higher ground. Comparison, from diverse non-calcareous areas of pH determinations of surface samples, taken from the soils of the upper parts of slopes and from the base of these slopes, are indicative of this nutrient drift, which in the alluvial mud itself is cumulative:

Geological character and county	pH of surface soil of slope above	pH of surface soil at foot of slope
London Clay, Hertfordshire	4.9 to 5.2	5.5
London Clay, Middlesex	5.5 to 5.7	6.9 to 7.1
Millstone Grit, Devonshire	6.1 to 6.4	6.7 to 6.9
Old Red Sandstone, Somerset	4.9 to 5.8	5.3 to 6.4
Ludlow Shales, Shropshire	5.6 to 5.8	6.5 to 6.7
Ludlow Shales, Herefordshire	5.4 to 5.8	6.2 to 6.5
Granitic, Cornwall	3.8 to 6.2	5.5 to 7.6
	av. 5.43	av. 6.77

Most of the species commonly met with on exposed muds exhibit a wide range of tolerance with respect to the pH. Some species are, apparently, normally calcifuge, as for instance *Ranunculus omiophyllus Elatine* spp. *Montia chrondrosperma*, *Peplis portula*, *Polygonum minus* and *Damasonium alisma*. But several species, though most commonly encountered on light sandy soils that may be acid in reaction, nevertheless also occur on sands with a neutral or alkaline reaction, even if calcareous. This is true of *Radiola linoides*, *Anagallis minima* and *Cicendia filiformis*. The normal restriction of *Pulicaria vulgaris* to acid sandy soils is perhaps largely due to the aggravation on these of competition pressures (cf. Salisbury 1967*c*, p. 711). The two species of *Bidens* are both to be met with on muds with a reaction above pH 7 but *B. cernua* appears to be the more tolerant of high pH values and is less a feature of acid sandy areas than *B. tripartita*. That soil texture does not play a direct role is indicated by the occurrence, in Hertfordshire, of *B. cernua* especially in ponds on the calcareous 'Clay-with-Flints' whilst *B. tripartitus* is a feature of the ponds on the 'London Clay' which is deficient in bases. Lhotska's (1968) studies of the genus *Bidens* in Czechoslovakia have indicated that the speed of germination can be an important factor in competitive efficiency and that *B. tripartita* is more tolerant of prolonged drought than *B. cernua* which may influence the greater prevalence of the former species on the less-retentive sandy soils.

When drought conditions impose a depauperate state upon these pioneer species the reproductive potential of an individual is inevitably very small (e.g. dwarf plants of *Chenopodium rubrum* with only 3 to 22 seeds), yet tests of seeds from such plants appear to indicate that, though the output is so meagre, there is not normally any diminution in their viability. It is quantity only and not quality that suffers. Further evidence of the wide tolerance of 'mud-species' in relation to water supply is provided by *Lythrum hyssopifolia* as a, not infrequent, cornfield casual and *Corrigiola littoralis*, in various counties, on railway tracks, sometimes in abundance (Kent 1959).

Mrs Esplan has called my attention to the occurrence of *Crassula tillaea* as an abundant and persistent weed of a tennis court and a fruit-orchard, both on sand. The endurance of such abnormal habitats may, it is suggested, be consequent upon the artificial suppression of competitors in these situations, so that the open character may be said to compensate for environmental defects in other respects.

A striking feature of the mud flora is that so high a proportion of the species are particularly associated with soft waters, especially those with a good supply of plant nutrients, and this preference may well be associated with their intolerance of competition. Several of these species when grown in isolation have been found to flourish on soils containing calcium, and parallel cultures, watered with hard water and soft water respectively, of *Ranunculus tripartitus* var. *terrestris*, *R. hederaceus*, *Scirpus setaceus* and *Elatine hexandra* have shown their tolerance of hard water when other species are not present. The necessity of calcium for the calcium pectate of cell-walls would imply that more robust competitors might be greatly handicapped by a paucity of calcium ions in the soil solution.

Significant quantitative assessments of the effects of competition are very difficult to obtain since, although the germination of the 'mud-species' is usually quasi-simultaneous, that of their competitors is not. Sowings of equal numbers of seeds from the same plant of *Veronica anagallis-aquatica*, with varying numbers of the grains of *Poa annua*, showed a reduction of from 21 to 45 % in the average fresh weight of the seedlings in the presence of the competitors compared with the fresh weight in their absence. However, probably owing to the great diversity in the rate of growth of the individual *Poa* seedlings, there was no appreciable correlation between the percentage diminution and the number of competitors. Even when the total mixed population was low in density a high density pure stand of the *Veronica* seedlings exhibited about 50 % better average growth.

The association of 'mud-flora' species with open habitats is patent evidence, not merely of their intolerance of competition but of their incapacity to exert significant 'infection pressure' on competitors, either by their habit of growth or the by-products of their activities. It is doubtless this inagressiveness that accounts for the high density that almost pure stands of these species sometimes attain on bare mud. *Anagallis minima* seedlings, for example, were found around the dead parent in May attaining a density of no less than 75 per square centimetre, and *Radiola linoides* can exhibit similar densities, whilst fruiting plants of *Limosella aquatica* have been found averaging five to the square centimetre. In the light of these facts the marked influence of soil conditions on the balance of competition is to be expected.

The alga, *Botrydium granulosum*, often occurs, as already stated, in great abundance on these exposed muds as the primary colonizer, not infrequently followed by the hepatic, *Riccia crystallina*. Other cryptogams sometimes present as mud colonizers of peaty pools are *Pilularia globulifera* and *Lycopodium inundatum*, both characterized by seasons of striking abundance or paucity. Nevertheless, they have probably gone permanently from over 60% of their former habitats. In similar situations and exhibiting similar fluctuations *Drosera intermedia* may be locally abundant though its permanent diminution may not be more than 20% of its recorded habitats.

It is arguable whether *Veronica beccabunga* and *Mentha pulegium* should be included in this category though, if so, both successfully withstand subsequent successional competition. In this context it is relevant to note that the latter species was dominant in a wet pasture near Lough Beg that was formerly a lake floor (cf. Steward & Corry 1938), and both species have been found as pioneers colonizing freshly exposed and marginal muds. *Ludwigia palustris* may well belong also to this community. It too occurs as a pioneer, has a high seed output and other features in common with these 'mud-species' but its rarity has precluded a satisfactory assessment of its status. On mud it may behave as an annual, though perhaps normally perennial. Mention should also be made of three perennial species of which, though not normally to be regarded as pioneers on mud, large numbers of seedlings have been observed, at an early phase of the mud succession, in one or two localities. These are: *Alisma plantago*, *Baldellia ranunculoides* and *Butomus umbellatus*. The last two may exhibit a pronounced development of root-hairs upon the collet (see seedling of *B. ranunculoides*, figure 23).

The very striking decrease in the natural habitats for these 'mud-species' throws into greater prominence their occurrence in artificially created environments such as cart-ruts and ill-drained cornfields (e.g. *Myosurus*, *Montia chrondrosperma*, *Limosella aquatica*). Where the natural habitats no longer remain, 'relict associations' may, as Braun-Blanquet (1932) has pointed out, be restricted to artificial conditions.

Myosurus minimus in Britain may be a colonist, brought in with early agriculture, as it occurs but rarely in natural habitats, most British records being from arable land subject to winter inundation, or cart-ruts. In Central Europe it is a pioneer on the naturally exposed mud along the margins of rivers rendered bare by a fall in the water-level. Here, as recorded by Hegi (1916, p. 540), it is associated, *inter alia*, with a number of other members of the 'mud-flora', namely: *Cyperus fuscus*, *Elatine hexandra*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Limosella aquatica*, *Lythrum hyssopifolia*, *Pilularia globulifera* and *Scirpus setaceus*.

From table 1, in which some fifty phanerogams of exposed mud are listed, it will be apparent that they exhibit a very wide taxonomic diversity, twenty or more Families are represented, so that shared characteristics cannot be attributed to affinity of descent but as evidence of 'natural

TABLE 1. 'MUD-SPECIES' FOUND AS PIONEERS, COLONIZING PREVIOUSLY SUBMERGED SOILS

species	vice-comital (% England)	decrease (%)	height or spread (cm)	observed fl. period	duration ( ) less f.
RANUNCULACEAE					
Myosaurus minimus	41	−75	4 to 16	III to VII	A.
Ranunculus hederaceus	100	−12	4 to 40	IV to XI	A. or (P.)
R. omiophyllus (*lenormandii*)	56	−14	15 to 50	II to XI	A. or (P.)
R. ophioglossifolius	2.6	−25	10 to 40	V to VII	A.
R. sceleratus	94	−?	10 to 120	IV to XI	A. or (B.)
R. tripartitus v. *terrestris*	14?	−55?	5 to 30	V to X	A. or ? (P.)
CRUCIFERAE					
Rorippa islandica	83	−?	7 to 100	VI to X	A. (or B.)
ELATINACEAE					
Elatine hexandra	28	−57	2.5 to 10	VI to X	A. (rarely P.)
E. hydropiper	7	−45	2.5 to 10	VII to VIII	A.
CARYOPHYLLACEAE					
Myosoton aquaticum	56	−3	10 to 45	V to X	A. or P.
ILLECEBRACEAE					
Corrigiola littoralis	1.7	?	5 to 25	VII to X	A.
Illicebrum verticillatum	3.5	−36	5 to 20	VII to IX	A. or (B.)
PORTULACACEAE					
Montia chrondrosperma	49	−?	2 to 7	IV to V and IX to X	A. or (P.)
CHENOPODIACEAE					
Chenopodium rubrum	71 (but mostly from artificial habitats)	−?11	1 to 125	V to XI	A.
LINACEAE					
Radiola linoides	83	−42	1.5 to 8	VI to X	A. or (B.)
CRASSULACEAE					
Crassula tillaea	9	−43	2.5 to 10	IV to IX	A.
LYTHRACEAE					
Lythrum hyssopifolia	13	−95	10 to 35	V to X	A. or (B.)
Peplis portula	93	−?	4 to 25	V to X	A. or (P.)
CALLITRICHACEAE					
Callitriche stagnalis	100	−?	2 to 8	IV to X	A. or (P.)
POLYGONACEAE					
Polygonum hydropiper	96	−?	25 to 100	VI to X	A.
P. minus	59	−67	5 to 50	VII to X	A.
P. nodosum	51	−16	10 to 70	VI to X	A.
Rumex maritimus	51	−43	7 to 100	VI to IX	A. or (P.)
R. palustris (*R. limosus*)	28	−32	7 to 120	VII to X	A. or (B.)
PRIMULACEAE					
Anagallis minima	67	−33	2 to 7	VI to X	A. or (B.)
Samolus valerandi	75	−?	5 to 90	VI to X	P. or (A.)
GENTIANACEAE					
Cicendia filiformis	9	−42	1.5 to 12.5	V to X	A.
SCROPHULARIACEAE					
Limosella aquatica	50	−82	2 to 5	VI to X	A.
L. subulata (*L. australis*)	2.6	?	2 to 4	VI to X	A.
Veronica anagallis-aquatica	?	?	20 to 80	VI to IX	P. or A.
V. catenata	57	−3.4	10 to 50	VI to VIII	P. or A.
V. scutellata v. *villosa*	42	−?	7 to 40	VI to IX	P. or (A.)

TABLE 1 (*cont.*)

species	vice-comital (% England)	decrease (%)	height or spread (cm)	observed fl. period	duration ( ) less f.
COMPOSITAE					
Bidens cernua	80	−21	4 to 150	VI to X	A. or (B.)
B. tripartita	80	−13	15 to 90	VII to X	A. or (B.)
Gnaphalium uliginosum	100	− ?	4 to 25	VII to X.	A.
Pulicaria vulgaris	21	−94	5 to 50	VII to IX	A.
ALISMATACEAE					
Damasonium alisma	13.4	−85	5 to 30	VI to VIII	A. or P.
JUNCACEAE					
Juncus bufonius	100	− ?	3 to 25	V to IX	A.
J. capitatus	2.6	−30	1 to 10	V to VIII	A.
J. mutabilis (*J. pygmaea*)	0.9	?	2 to 15	V to IX	A.
CYPERACEAE					
Cyperus fuscus	5.2	−55	3 to 20	VII to IX	A.
Eleocharis parvula	4.4	?	2 to 8	VII to IX	P.
Scirpus setaceus	99	− ?	10 to 20	VI to X	A. or (P.)
GRAMINEAE					
Alopecurus aequalis (*A. fulvus*)	34	−23	10 to 35	V to IX	A. (or B. or P.)
A. geniculatus	100	?	15 to 45	VI to IX	P.
The following, potentially perennial species, may also occur:—					
Eleocharis acicularis	70	−58	2 to 20	VII to IX	P. or (A.)
Littorella lacustris	86	−13	2 to 25	V to X	P.
Ludwigia palustris	1.9	−50	5 to 30	VI to VIII	A. or P.
Mentha pulegium	46	−76	10 to 30	VII to X	P.
Veronica beccabunga	100	?	10 to 50	V to IX	P.

selection', under peculiar environmental conditions, of organisms possessing similar potentialities. Whilst these species exhibit little in common as to habit of growth they roughly comprise two groups. Twenty-four of the species are of low stature, are usually annuals, and most are associated especially with the shallower inundations, which often implies the smaller ponds or pools. Two dwarf perennial species, doubtfully attributed to this community, are: *Littorella lacustris* and *Eleocharis acicularis*. The former can flourish at depths of over 2 m, around the edges of lakes and reservoirs, where it multiplies by vegetative spread, but only when it is emersed does it become fertile. This suggests that the submerged state is secondary. *Eleocharis acicularis* also is similarly sterile in the submerged condition but, when emersed, fruits freely in very dry seasons (de Tabley 1899, p. 315). An almost equal number of species constitutes the other group. These can, and normally do, attain an appreciable stature. They include a small proportion that can be perennial, although on the bare mud they often behave as annuals. These two potentialities, of greater height and duration, are features which enable those particular species to tolerate a greater degree of competition and, if the circumstances of vegetational succession permit, they persist longer, in contrast to the low-growing annuals which are quickly eliminated where plant succession is not inhibited.

The recurrence of a species, in any one locus, may be annual, or may be irregular with intervals of, perhaps, many years, and this applies to the members of both groups equally. With but few exceptions these species exhibit, in varying degrees, a fluctuation of population numbers that is outstanding even for annuals.

The population fluctuations of some of these 'mud-species' over a period of 9 years have been recorded by Gross (1942) at Coate Water, in Wiltshire. *Bidens tripartita*, for instance, was scarce in 1934 but was abundant 2 years later and then declined, becoming once again common in 1938. *Alopecurus aequalis* which was abundant in 1934 declined to scarcity in 1936 but in 2 years was again common, yet once more became scarce in 1940. Since both species were common in 1938 reciprocal competition cannot be invoked.

The vice-comital percentages (table 1, column 2) show that some species are widespread, and of these *Callitriche stagnalis*, *Gnaphalium uliginosum* and *Juncus bufonius* are almost ubiquitous in suitable habitats. Others which occur widely may nevertheless be very unevenly dispersed, as for example *Ranunculus hederaceus* and *Scirpus setaceus*. The majority of these 'mud-species' are, however, very localized and, though often exhibiting a considerable degree of climatic tolerance, would appear to be markedly sensitive to edaphic conditions, though whether this be a direct effect or an indirect effect through the influence of soil conditions on competitive efficiency is, in most instances, problematical.

A number of these 'mud-species' are designated in the *Floras* as 'rare', some, such as *Elatine hydropiper* and *Cyperus fuscus* as 'very rare', yet most have occurred in some particular year, or years, exhibiting an abundance that is quite phenomenal (e.g. *Elatine hydropiper* near Droitwich in 1919; *Cyperus fuscus* near Cleveden in 1900: *Rumex palustris* near Hendon in 1921, *Limosella aquatica* near Tring in 1919).

Owing to the locally restricted occurrence, it is in no degree surprising that in any single locality only a small proportion of the plants listed in table 1 are encountered. Of the species that do occur together in the same locality, moreover, some may be present one season and then perhaps are not seen again for a period of years, whilst from a number of localities species formerly present have long since been absent. Though this may often indicate extinction it could merely represent prolonged abeyance.

The useful separate presentation, in the *Atlas of the British Flora* of records made prior to 1930, but not since confirmed, permits of a surmise as to the diminution of occurrence. This is tentatively presented (in table 1, column 3) as a percentage decrease. Whilst, because of possible reappearance, the actual figures should only be regarded as indicative, it will be obvious, at once, that the most characteristic species exhibit what appears to be a very marked diminution of frequency. An average for all those for which data are available, suggests a general reduction of over 40%. However, for a few species, the probable decrease has been particularly severe, notably for *Damasonium alisma*, *Pulicaria vulgaris*, *Lythrum hyssopifolia* and *Limosella aquatica*. These four are primarily species met with on muds of the smaller areas of water for which, perhaps, the most important single factor affecting decrease has been the augmenting neglect of ponds in fields and their disappearance from waysides, since ponds no longer play an important role for the watering of stock, either on the farm or in transit by road. From the time, more than two centuries ago, of the boggy trackways, so vividly described by Defoe, when these must have provided a wealth of suitable habitats for the 'mud-species', such wayside quagmires have rapidly diminished. Trevelyan in his *Social history* has stated that already by 1840 there were 22000 miles of good turnpike roads in England and, to-day, the small residue of roadside ponds commonly suffer some pollution from the 'tarred' road surfaces, whilst 'piped water' has rendered the field-ponds widely redundant for the farmer, so these are permitted to become choked by natural succession or are filled in and obliterated.

It must be recognized that, in some respects, distribution recorded by presence in, or absence from, squares of 10 km is a very crude method of presentation, since there is no discrimination between occurrence of a few individuals, in a single spot, and that of numerous invididuals, in many localities, scattered throughout the square. Or, again, between high frequency throughout an area of about 150 sq. miles and localized occurrence around the meeting-point of four 10 km squares. Even allowing for such sources of error, the actual diminutions are probably in excess of these tentative estimates since the losses of suitable habitats, especially wayside and field ponds, have been greatly accelerated during the past 39 years.

The chief causes for the diminution of a species may be either general, or special. To the former category belong the decrease of suitable habitats resulting from increased drainage and lowering of the water-table or the disappearance of ponds due to the causes just cited. Special causes of decrease are augmented predation and incidence of disease as well as the miscellaneous hazards to which individual species are subject. The general factors will manifestly tend to affect all species of similar habitat requirements almost indiscriminately, whilst the special factors will affect each species differently and any augmentation of such will inevitably tend to be less severe the larger the average reproduction of the species. Plotting the estimated decrease of frequency of 21 of these 'mud-species' against the logarithm of the estimated average seed, or fruit, output of each, it is apparent (figure 1) that there is little if any significant correlation between potential reproduction and the degree of diminution, which clearly suggests that the causes of decline are general and not special.

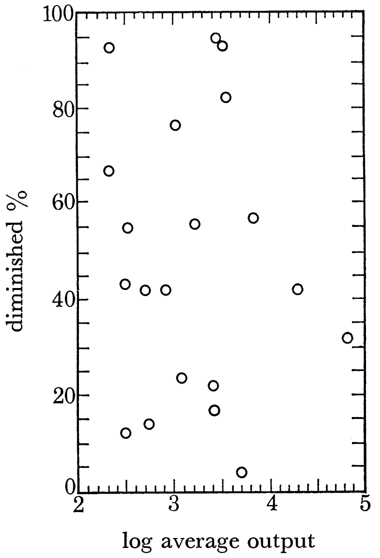

Figure 1. The probable percentage diminution of twenty-one 'mud-species' plotted against the logarithms of their average seed (or fruit), outputs in a year.

Provenance and distribution

The higher temperatures of southern climes and the more extreme conditions of continental areas are clearly favourable to the high evaporation rates upon which the habitats of the 'mud-species' so largely depend. It is therefore no surprise that the provenance of a large proportion of these species is either continental (e.g. *Elatine* spp., *Limosella aquatica*, *Polygonum minus*, *Rumex palustris*) or continental-southern (e.g. *Corrigiola littoralis*, *Cyperus fuscus*, *Lythrum hyssopifolia*). Others are southern-oceanic types (e.g. *Crassula tillaea*, *Damasonium alisma*, *Juncus mutabilis*).

These geographical relationships are similarly indicated by the distribution trends within the British Isles themselves. Forty per cent of the 'mud-species' are conspicuously southern in their occurrence and most of these are absent from Ireland and either rare, or absent, from Scotland (e.g. *Alopecurus aequalis*, *Cyperus fuscus*, *Damasonium alisma*, *Illecebrum verticillatum*, *Juncus mutabilis*, *Ranunculus ophioglossifolius*). A further thirty-seven per cent are species which exhibit a definite trend of increasing frequency towards the south (*Myosoton aquaticum*, *Polygonum nodosum*, *Ranunculus omiophyllus*, *Rorippa islandica*). Only about twenty percent are of general occurrence in the British Isles or exhibit no obvious trend (e.g. *Callitriche stagnalis*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Polygonum hydropiper*).

It is of interest to note that amongst the species listed by M. Flahault (1893, p. 92) as being characteristic of depressions subject to winter inundation in the South of France are the following: *Myosurus minimus*, *Lythrum hyssopifolia*, *Pulicaria vulgaris*, *Cyperus fuscus*, *Juncus bufonius* and *Juncus pygmaeus*. Massart (1910) describes a comparable marginal society in Belgium.

On the European mainland there occur, as one would expect, associated with members of our own 'mud-flora', additional species which are characteristic and which exhibit a geographical distribution that tends to stress the features here adumbrated. For instance *Juncus tenagea* is a species of middle and southern Europe whilst *Lindernia pyxidaria* and *Elatine triandra* are essentially central European. It is also relevant to note that the following 'mud-species' are recorded, by Black (1948–57) from South Australia: *Anagallis minima*, *Cicendia filiformis*, *Juncus capitatus*, *Lythrum hyssopifolia*, *Myosurus minimus*, *Rorippa islandica*, *Samolus valerandi* and *Veronica anagallis-aquatica*.

The striking localization of these 'mud-species' naturally diminishes greatly the chance of their presence in the subfossil deposits that have been examined. The rise of temperature in the interglacial period may well have been favourable to the provision of suitable habitats. It is therefore of interest to note that Clement Reid (1899), in his pioneer studies of the history of our flora, records the following species from deposits of this period: *Bidens tripartita*, *Elatine hydropiper*, *Eleocharis acicularis*, *Limosella aquatica*, *Ranunculus hederaceus*, *R. sceleratus*, *Rumex maritimus* and *Scirpus setaceus*. More recent studies have added *Pilularia globulifera* and perhaps *Cicendia filiformis* to the list (Godwin 1956).

Damasonium alisma has been found in a glacial deposit whilst the Late Glacial has yielded *Callitriche stagnalis*, *Rorippa islandica* and *Veronica anagallis-aquatica*. *Juncus bufonius* and *Ranunculus omiophyllus* have not been recorded earlier than the Neolithic. Bronze Age deposits have yielded *Lythrum hyssopifolia*, *Polygonum hydropiper* and *P. minus*. *Chenopodium rubrum* is recorded from the Iron Age and *Bidens cernua* not till Roman times. However, in view of the small number and the diversity of associated 'mud-species' in any one habitat at the present day, the absence of species from particular subfossil deposits may be without any significance.

Flowering and fruiting

High evaporation rates and low precipitation being normally a feature of the later summer months, it is during the period from July to October that water-levels are predominantly low. It is therefore of interest to note that the prevailing periods of flowering for the mud flora are July and August, when about 90 % of the species may be in bloom whilst about 54 % may extend their flowering into October. The autumnal bias in flowering is well shown by comparison with the flowering periods of aquatic and of the wet-meadow flora (see figure 2). Thus mature fruits are mostly shed between mid-August and October, the period when habitats suitable for colonization are most likely to recur.

Chenopodium rubrum affords a particularly instructive example in this context. First, however, it should be emphasized that this species, though most familiar as a casual weed, or denizen, of dung-heaps and rich garden soils, would appear to be a natural occupant of alluvial muds, especially those with a high organic content. When mud exposure occurs early in the year *Chenopodium rubrum* seedlings, under the influence of the short nights and long days of summer, flourish vegetatively but are slow to come into flower and attain a large size, although flower-formation occurs before the nights appreciably lengthen. From two such plants, growing on the mud of a pond, that had attained a height of over 90 cm, the seeds were carefully harvested and cleaned and, with the aid of several aliquot samples in which the seeds were actually counted, the number of seeds in the whole crop was estimated by weight. For the one individual the seed output was over 327000, and for the other over 586000. Both, be it noted, are slight under-estimates, since some seeds were inevitably lost in the process of cleaning. When, however, mud exposure occurs late in the year, the long night and short days have a remarkably accelerating effect upon the maturation of the seedlings of this species, as has been shown experimentally (Cumming 1959). In November 1959 stretches of mud of a reservoir near Tring were carpeted with miniature plants of *C. rubrum* (figure 9 E. E.), many with but two leaves and the cotyledons. Nevertheless, they bore from 5 to 22 fruits of which a large proportion were ripe, although the plants were probably not more than 2 to 3 weeks old. This example sufficiently attests the remarkable plasticity and adaptability of, at least one of, these 'mud-species' to meet the changes of this environment. *C. rubrum* has been referred to as a 'short-day' plant (Schwabe 1968), but

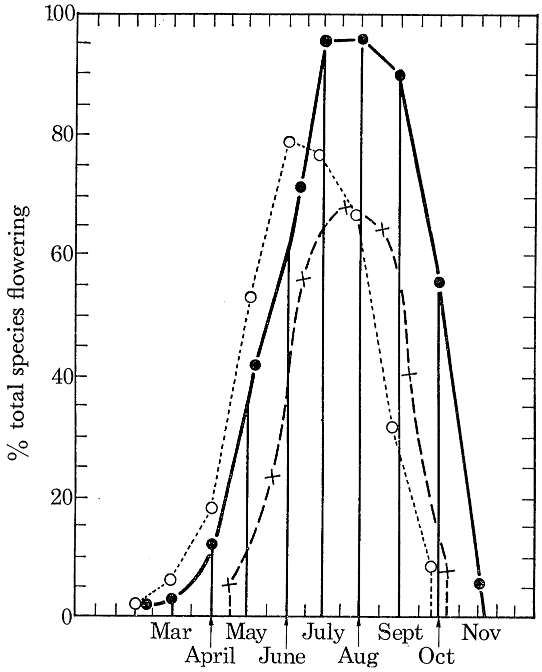

FIGURE 2. Flowering seasons of the 'mud-species' compared with those of the wet-meadow and wet-grassland species, as well as those of aquatic plants. Ordinates represent percentages of the total species flowering in each month. Full-line = 'mud-species'; dotted line = wet-meadow and -grassland species; dashed line = aquatic-species.

this is misleading since it has been found coming into flower during the long days and shortening nights of May and June, as well as, far more rapidly, during the lengthening nights of September. Since, as can be seen from table 1, many of these 'mud-species' may be found in bloom in the height of summer as well as in the autumn, it is unlikely that the incidence of their flowering is photoperiodically determined unless separate strains, with different responses, be involved, although the acceleration of flower initiation, as with *C. rubrum*, may be influenced. That the prolonged flowering is not the outcome of initiation at one day-length followed by extension into another, is indicated by the flowering of a number of these species, in cultivation, sown at different periods. Nevertheless, the possibility of polybiosis (see p. 250) with respect to day-length remains.

A number of these 'mud-species' successfully fruit in the submerged state, when the flowers are pseudo-cleistogamous. Comber (1965) found that when shoots of *Veronica anagallis-aquatica* were completely immersed pseudo-cleistogamous flowers developed, which produced fertile seeds. Such submerged fruits of this and other species normally contain fewer seeds and the submerged plants fruit much less freely. There is good evidence that, for some species at least, the emersed state is that for which these plants are best adapted (for the evidence re *Elatine hexandra* cf. Salisbury (1967*a*)). The marked reduction in seed output of the submerged plants is often accompanied by an augmented life-span. From the data provided in table 2 it will be seen that the estimated seed production, of all but the smallest mud species, can attain to thousands and that, in common with species characteristic of other 'intermittently available' habitats, they are highly prolific. It is to be noted that this abundance, particularly of emersed individuals, is often quite remarkable in relation to the size of the plant and, for the normally annual species, fruiting is soon followed by death. But this sequel often ensues after prolific fruiting for those species which are potentially perennial.

The small size, copious fruiting and monocarpic habit of *Callitriche stagnalis* plants, when emersed upon mud, is familiar. Other potentially perennial species which are often annual or short-lived, on the exposed mud include: *Damasonium alisma*, *Myosoton aquaticum*, *Ranunculus hederaceus*, *Ranunculus omiophyllus* and the *Veronica* species *V. anagallis-aquatica*, *V. catenata* and *V. scutellata* var. *villosa*.

With some other species, normally regarded as annuals, the converse circumstances may obtain. Thus seedlings of *Elatine hexandra* developing on exposed mud and then covered by water are enforcedly cleistogamous, which implies a much reduced production of seeds. Such plants I have known to perennate and fruit annually over a period of 3 years. *Alopecurus aequalis* on bare mud is normally annual but, in shallow water, may become biennial, or even perennial. In general all the most characteristic species of these exposed muds are either annuals, or species which though potentially perennial, in these specialized environments become of short duration or even predominantly annual.

Statements as to the duration of species in *Floras* are often inadequately based upon field observations, or even mere repetitions. *Damasonium alisma*, for example, is stated in most *Floras* to be perennial, without qualification, although on exposed mud it may certainly be annual. Trimen & Dyer, in the *Flora of Middlesex* (p. 286), and Boswell Syme, in *English Botany* (**9**, p. 75), writing a century ago when this species was far more frequent than now, both designate this species as perennial *with a query*. Recent *Floras* are less wise. It has been alleged that the variety *villosa* is a mere environmental state of *Veronica scutellata* doubtless because the type and the variety are commonly found in distinctly different environments, a fact on which Druce

TABLE 2. ESTIMATES OF THE AVERAGE AND EXCEPTIONAL PROPAGULE PRODUCTION OF SPECIES OF BARE MUD (To nearest round number)

species	av. weight of seed or fruit (mg)	observed range of height or spread (cm)	estimated av. of seed output in 1 year	est. output of largest plant found in fruit	ratio, max./av.
A. Taller types (most individuals exceed 25 cm)					
Chenopodium rubrum(1)	0.09	1 to 125	*ca.* 176000	586000	3.3
Rumex palustris (= *limosus*)	0.43 (fr.)	7 to 120	*ca.* 64000	over 200000	3.0
Veronica anagallis-aquatica	0.027	20 to 80	53860 ± 7100	191760	3.5
Rorippa islandica(2)	0.076	7 to 100	33000 ± 7400	152000	4.6
Ranunculus sceleratus(3)	0.132 (fr.)	10 to 120	28000 ± 2700	120000	4.2
Veronica catenata	0.036	10 to 50	22760 ± 2460	87000	3.8
Myosoton aquaticum	0.19	10 to 45	5410 ± 670	27720	5.1
Pulicaria vulgaris	0.162 (fr.)	5 to 50	2710 ± 133	over 16000	5.9
Polygonum nodosum	1.8 (fr.)	10 to 70	2700 ± 1360	*ca.* 25000	9.3
Bidens cernua	3.2 (fr.)	4 to 150	2600 ± 220	35460	13.6
B. tripartita	3.4 (fr.)	15 to 90	1670 ± 160	8400	5.0
B. Low-growing types (most individuals under 15 cm)					
Juncus bufonius	0.15	3 to 25	16980 ± 1436	175200	10.3
Gnaphalium uliginosum	0.059 (fr.)	4 to 25	12760 ± 1500	119090	9.3
Peplis portula	0.0455	4 to 25	7660 ± 1055	21580	2.8
Elatine hexandra	0.03	spread 2.5 to 10	6700 ± 51	27000	4.0
Samolus valerandi(4)	0.026	5 to 90	3980 ± 306	29300	7.3
Limosella aquatica	0.0097	2 to 5	3600 ± 5	12950	3.5
Lythrum hyssopifolia	0.117	10 to 35	2550 ± 13	74500	29.0*
Alopecurus aequalis	0.14	10 to 35	1240 ± 93	4160	3.3
Juncus capitatus	0.0068	1 to 10	1140 ± 147	7000	6.1
Myosurus minimus	0.03	4 to 16	1040 ± 40	3100	3.0
Ranunculus ophioglossifolius	0.37 (fr.)	10 to 40	820 ± 70	3080	3.7
Radiola linoides	0.01	1.5 to 8	770 ± 70	5570	7.1
Cicendia filiformis	0.003	1.5 to 12.5	510 ± 37	2760	5.4
Ranunculus omiophyllus (= *lenormandii*)	0.52 (fr.)	15 to 50	520 ± 20	1320	2.5
R. hederaceus	0.37 (fr.)	4 to 40	430 ± 37	2150	4.9
Polygonum hydropiper	2.5 (fr.)	25 to 100	426 ± 62	2730	6.4
Cyperus fuscus	0.145 (fr.)	3 to 20	310 ± 64	4470	14.4
Crassula tillaea	0.012	spread 2.5 to 10	290 ± 16	1700	5.8
Juncus mutabilis (= *pygmaeus*)	0.02	2 to 15	260 ± 38	700	2.7
Anagallis minima	0.036	2 to 7	250 ± 24	6380	25.8*
Damasonium alisma	1.52	5 to 30	230 ± 15	1510	6.5
Polygonum minus	0.78 (fr.)	5 to 50	210 ± 10	2630	12.5
Scirpus setaceus	0.138 (fr.)	5 to 20	154 ± 12	1380	9.8
Ranunculus tripartitus var. *terrestris*	0.5	5 to 30	103 ± 6	400	3.9
Montia chrondrosperma	0.3	2 to 7	81 ± 10	840	10.3

	av. wt. of propagules	av. growth	av. output	average ratio m/a
11 larger species	0.85	58 cm	*ca.* 36000	5.6
25 smaller species	0.308	17.1 cm	*ca.* 3570 ± 160	7.7 (or omitting*, see text, 6.0)

(1) An isolated specimen of *Chenopodium rubrum* has been known to attain 200 cm.
(2) *Rorippa islandica* is stated to attain to 190 cm in California (Jepson 1951).
(3) *Ranunculus sceleratus* is recorded by Trail (1923) as growing on ballast under 2 in high but fruiting.
(4) *Samolus valerandi* was found by Marshall (1914), growing in a swamp, up to 3 ft high.

Illecebrum verticillatum was found to exhibit a very wide range of size and fruitfulness. Most plants on mud were small but one large plant had produced over 2700 fruits. However, the data were judged inadequate to provide even an approximate average.

(1897) commented, and which my own experience confirms, but the two are occasionally to be found growing intermingled. The type flourished in situations where the plants are, in large part, submerged throughout the year, whilst the var. *villosa* is typical of situations normally subject to winter inundation only. Both taxa, alike, fruit most freely when aquatic conditions are in abeyance and may fail to develop stolons and behave as annuals. Under drought conditions the average seed output appears to be very similar for both taxa. The type has been grown to maturity in soil with a very low water content but produced plants that were entirely glabrous, small, and short-lived.

Two species that exhibit a remarkably constant association are *Radiola linoides* and *Anagallis minima*. Although the former occurs in some localities without the latter, *A. minima* is very rarely, if ever, found where *Radiola* does not occur. It is therefore of considerable interest to note that the decline of the two species is approximately proportional to the frequencies of their former occurrence. The 'reproductive capacity' of *A. minima* is about one third that of its associate.

The more adaptable species, such as *Juncus bufonius*, *Gnaphalium uliginosum*, *Ranunculus sceleratus*, *Peplis portula*, *Rorippa islandica* and the two species of *Bidens* are still widely encountered, but species such as *Rumex palustris* and *Chenopodium rubrum*, despite their high reproductive potentials, are infrequent though locally abundant.

Reproductive potentials

In table 2 the estimated average production of fruits or seeds for 36 species are enumerated. The size of the random samples available, on which these averages are based, varied greatly but the 'probable errors' enable one to gauge the reliability of these assessments. The high productivity in relation to the size of the plants is very obvious, particularly with respect to some of the smaller species. The absence of any obvious correlation between frequency and output of these 'mud-species' provides further evidence that their restriction is due to the rarity and decline of suitable habitats. With respect to the data for *Chenopodium rubrum* it must be emphasized that these are based upon the tall summer plants. The small plants of the late autumnal populations would, of course, yield a very low average. The striking feature of this seasonal dimorphism is that very large populations of both types may occur, but usually one or the other, according to the climatic conditions.

In the fifth column of table 2 the estimated seed production of the largest fruiting specimen observed has been added and, though it might be thought that the output of these exceptionally vigorous invididuals is mainly a matter of chance, it is noteworthy that the ratio of the observed maximum to the average productivity (table 3, col. 6) for 32 of the 36 species, varies but narrowly, from 4.7 to 5.3 around an average ratio of 7.2.

With respect to four of the species, however, the ratio is strikingly different; *Bidens cernua*, 13.6; *Cyperus fuscus*, 14.4; *Anagallis minima*, 25.8; *Lythrum hyssopifolia*, 29. For these two last I have furnished data to show that, while most individuals are derived from spring germinations, in some seasons a small proportion are derived from autumnal seedlings and when these latter survive the winter they may exhibit exceptional fruitfulness, attributable to the more prolonged vegetative growth and assimilatory activity before flowering ensues (cf. Salisbury 1969). It is not improbable that the very prolific plant of *Bidens cernua* was also technically a biennial, since autumnal germination and winter survival is known to occur with this species.

Though *Damasonium alisma* is a potentially perennial species and the highest yielding specimen was perhaps more than 1 year old, yet the conditions which favour the perennial duration in this, as in other species, are not those conducive to prolific fructification. Of the taller species, *Veronica anagallis-aquatica*, *V. catenata* and *Myosoton aquaticum* are all potentially perennial but the ratios they present are, alike, close to the average.

The estimated output for the potentially perennial species is that for 1 year only, and thus comparable with the output of the single generation of an annual. The perennial species in other habitats sometimes increase their outputs year by year, as the size of the individual augments, though this productivity usually diminishes somewhat as the limiting life-span is approached. On the other hand, the perennial may often require one to several years to attain its optimum output, whereas the annual species may attain this yearly. Since, however, the potentially perennial species which occur as pioneers on exposed muds so often behave as annuals the yearly basis of comparison may be deemed appropriate.

The fact that these maximal estimates bear so similar a relation to their respective averages in most instances affords strong presumptive evidence that (1) they are extreme values in the

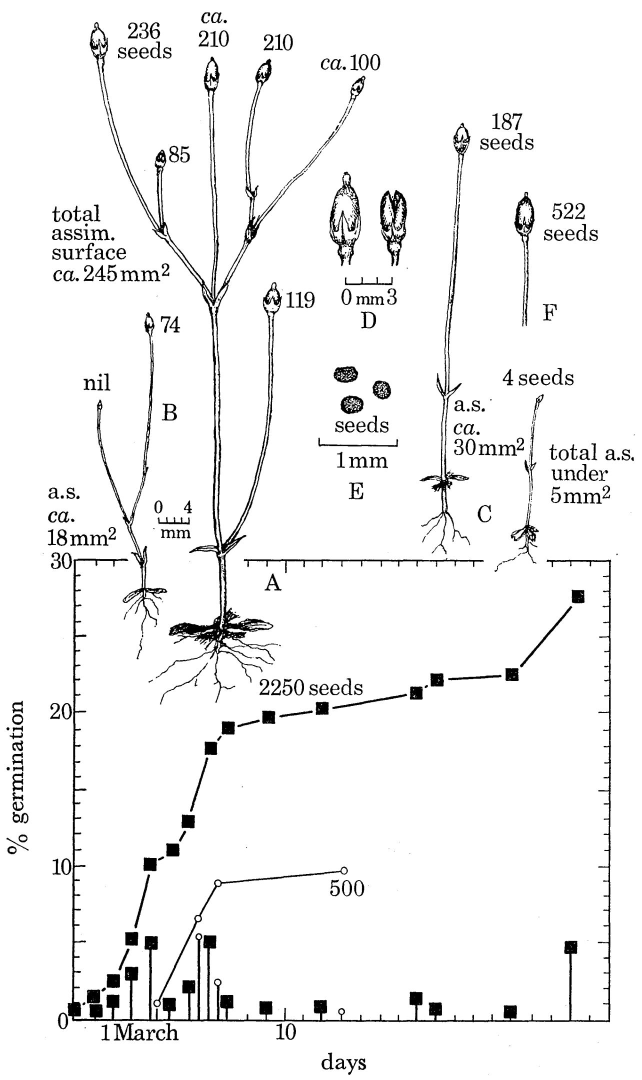

FIGURE 3. *Below*: graph of germination of seeds from plants of *Cicendia filiformis* ripe and sown in October, germinating in March. *Above*: drawings of plants showing the range in size of the assimilatory surface and of the seed contents of their capsules (A, B, C and F). D, mature and dehisced capsules; E, seeds.

normal variation but not abnormalities, also (2) that the averages themselves are probably fairly representative. Two species which most conspicuously fail to conform to this generalization have been shown to exhibit seasonal dimorphism, which invalidates the basis of comparison. *Damasonium alisma* is, surprisingly, a conformist despite the inclusion of data which, *faute de mieux*, are admittedly suspect of biased selection.

Cicendia filiformis is a species that exhibits a striking diversity in fruiting features. Nearly 800 plants derived from random samples in three localities and in more than one season were examined for the number of fruits. The average was 3.0 capsules (S.E.M. 0.13) but 489 plants had only one or two. About 7 % bore from 6 to 14 capsules. The range in seed content is conspicuous and in the accompanying figure 3 a range of examples is portrayed together with estimates of the assimilatory surface that the individual plants presented. This is provided by the basal rosette of leaves which are small and short-lived and the green axes which function for an appreciably longer period. When the plants are growing in a damp hollow on sand rich in organic material not only is the life of the rosette prolonged but the environment is very favourable to photosynthesis. The seeds were actually counted in 113 capsules and, in view of the marked diversity of contents, the results are recorded here:

number of seeds in capsule	number of capsules	number of seeds in capsule	number of capsules	number of seeds in capsule	number of capsules
4	1	135	1	241	1
22	1	136	1	242	1
26	1	137	1	244	1
29	1	147	1	246	1
31	1	154	1	248	1
35	1	156	1	250	1
42	2	161	1	253	1
45	1	165	1	260	1
46	1	169	2	267	1
47	1	170	1	271	1
50	1	171	1	274	1
51	1	176	2	276	1
54	1	181	1	278	1
56	2	182	1	279	1
58	1	186	1	291	1
67	1	187	1	297	1
69	1	190	2	301	1
70	2	192	1	306	1
71	1	193	1	308	1
74	1	197	2	321	2
77	1	200	1	333	1
85	1	205	1	340	1
88	1	210	3	358	1
90	1	216	2	430	1
100	1	219	1	431	1
103	1	221	1	441	1
112	1	224	2	453	1
114	1	227	1	469	1
115	1	228	1	491	1
119	1	232	1	493	1
125	1	236	1	597	1
129	2	237	2	635	1
133	1	238	2		

average 196.6 (S.E.M. 11.6)

There is no obvious 'mode' but the highest proportion of the capsules, nearly 45 %, contained seeds numbering between 154 and 250, so that the validity of the average is likely.

A number of germination tests have been made, involving thousands of seeds derived from more than one locality and harvested in different years, but a high percentage has never been attained. Frost has been claimed as a requisite for the germination of *Cicendia* so it is possible that its extreme localization in England may be associated with cold-air drainage and 'frost-pockets'. However, it must be admitted that years of high frequency have sometimes followed mild winters so possibly the period of after-ripening of the seeds in the soil is prolonged or abbreviated by climatic conditions according as these are less or more extreme.

The study of *Polygonum lapathifolium* and *P. nodosum* by Timpson (1965), has emphasized the difficulty of separating the populations of these. However, the segregate *P. nodosum* has been retained as emphasizing that the mud-plants considered here were characterized by the presence of numerous yellow glands, by the less obtuse 'dirty pink' inflorescences and the very swollen internodes, associated with this ill-defined segregate.

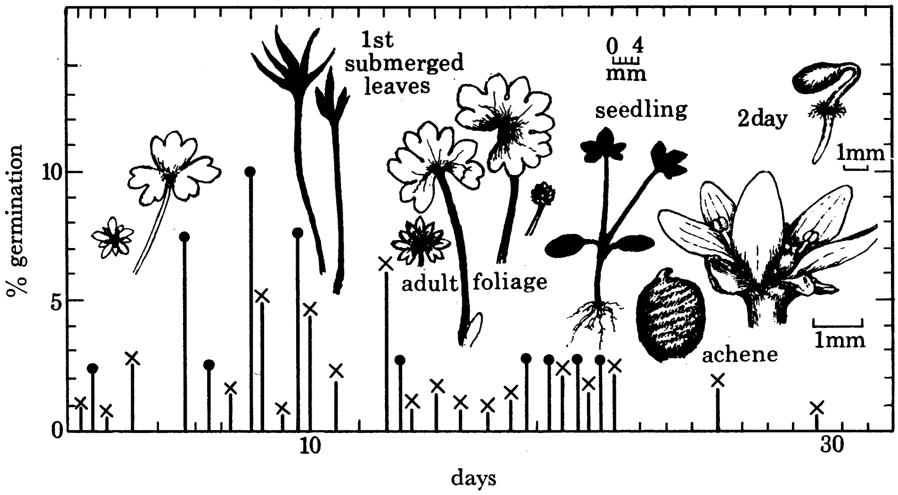

FIGURE 4. Daily germinations of two sowings of *Ranunculus tripartitus* var. *terrestris*. Ordinates represent percentages of seeds sown germinating on that day. Abscissae represent days from the first germination. *Inset:* flower and mature achene on the same scale. On right 2-day seedling showing 'prop-hairs'. Seedling showing cotyledons and first leaves also adult foliage. On left the first formed foliage leaves of submerged seedlings. ●, 40 sown 1 September 1967; ×, 200 sown 6 September 1968. Scale marks of insets show millimetres.

The plants here referred to as *Ranunculus tripartitus* var. *terrestris* include, in part, plants that have been designated *R. lutarius*. D. K. Cook has furnished evidence that the plants grouped under this latter taxon are probably of hybrid origin. Nevertheless, numerous sowings of achenes from several localities, of the mud-plants now under consideration, exhibited no recognizable segregation amongst the resultant offspring. Furthermore, seedlings submerged immediately after germination in no instance developed the dissected type of underwater foliage characteristic of typical *R. tripartitus*. Thus these mud-plants have identity of their own which is best emphasized by designating them var. *terrestris*. Still, to avoid ambiguity attaching to our mud taxon, salient features of flower, fruit and foliage are portrayed in figure 4. These terrestrial plants approach *R. tripartitus* s.s. in the small flower (usually under 6 mm diam.) and the small number of achenes in the fruit, and agree in the hairy receptacle, but differ, especially, in the absence of heterophylly when submerged. From the figures showing the first-formed leaves of the emersed and submerged seedlings of var. *terrestris* (figure 4) it will be apparent that those of the latter are but attenuated versions of the former and differ markedly from the trichotomously branched, filiform, submerged leaves of *R. tripartitus* itself.

A striking character of this taxon is the frequency of flowers with less than five petals, a feature exhibited very infrequently by *R. hederaceus* and not observed in *R. omiophyllus*.

The fruit size of these three taxons is distinctive. The number of carpels in the fruit is highest in *R. omiophyllus* ranging, in the numerous fruits examined, from 21 to 67 (average 38 ± 0.6). In *R. hederaceus* the range was from 6 to 43 carpels (average 21 ± 0.6) whilst *R. tripartitus* var. *terrestris* only produced from 3 to 24 carpels in the fruit (average 11 ± 0.2). Only 50 fruits of *R. tripartitus* s.s. itself have been examined, compared with between 150 and 375 fruits, in which the achenes were counted, of the other taxons. This rather small sample showed a range of from 3 to 18 carpels with an average of 9.6 ± 0.3. Its reproductive capacity is probably smaller than that of its putative hybrid.

The three white-flowered buttercups colonizing muds are all preferential calcifuges, but in varying degrees. *R. hederaceus* is tolerant of comparatively hard water, *R. omiophyllus* far less so, whilst *R. tripartitus terrestris* appears to be restricted to soft-water muds. It is to be noted that, even in the moister conditions of Ireland, *R. hederaceus* and *R. omiophyllus* are classified in the same order of calcifuge propensity (More 1898).

The two commonest and most widespread of the smaller 'mud-species', namely *Juncus bufonius* and *Gnaphalium uliginosum*, both exhibit an exceptionally wide range of size, from depauperate individuals bearing only a single capsule, or capitulum, to specimens producing over 1800. The remarkably large outputs in relation to plant size, that these species can exhibit, is naturally associated with very small propagules. The fruits of *G. uliginosum* var. *pseudopilulare*, when deprived of the pappus, have an average weight of only 0.006 to 0.015 mg, whilst the average weight of the seeds of *Juncus bufonius* ranges from 0.015 to 0.02 mg. This implies restriction to very open habitats and the capacity for rapid germination is a special asset. The common occurrence of these two species is no doubt largely due to the copious production of propagules but also to their tolerance of a wide range of soil conditions. With respect to this latter we may note that *Gnaphalium uliginosum* has been found flourishing on muds ranging in reaction from as acid as pH 4.2 to as alkaline as pH 8.4. *Juncus bufonius*, although most prevalent on soils that are appreciably acid (pH 4.0 to 5) can occur on alkaline soils also (pH 8.0).

Both *G. uliginosum* and *J. bufonius* may become dominant over appreciable areas and Eklund (1929) has estimated that the latter species may produce between thirteen and fifteen million seeds per square metre! It is scarcely surprising that *J. bufonius* has the widest distribution of its genus and 'is almost cosmopolitan' (Good 1947). It will be noted that the seed production of *Damasonium alisma* is the smallest of the potentially perennial species we have estimated. This was based upon the entire population that appeared on the mud of a dried-up pond, namely 64 plants together with a smaller number of plants from other localities (Salisbury 1942). It was therefore deemed desirable to test how far the average and distribution trend would be affected by the inclusion of data from entire specimens preserved in herbaria. The rarity of the species and the small size of the plants, appreciably diminish, though they do not eliminate, the selective character of herbarium specimens. Nevertheless, the result of including all these non-random data, yielding a total of 314 plants, is shown in the accompanying figure 5, from which it is seen that, though the range of fruit number is considerably extended, the form of the variation curve is not distorted. The average number of fruits is increased from 19 to 24. The random sample embraced approximately 75 % of individuals bearing less than 20 fruits while the larger assemblage contained approximately 60 % of such. From these figures we can, perhaps, conclude that the low seed output, so uncharacteristic of these 'mud-species', is a real feature of *Damasonium* *alisma* and not an illusion due to errors of sampling. The low reproduction rate of *Damasonium alisma* and the even smaller outputs of *Polygonum minus* and *Ranunculus tripartitus* var. *terrestris*, are, no doubt, correlated with the comparatively large size of their propagules, but the rarity of all three species is, in part at least, probably to be attributed to their low reproductive capacities. The germination of *Polygonum minus* is usually not more than about 60 %, implying a reproductive capacity of *ca.* 160. *Damasonium alisma* has only yielded very low germinations in my own tests but the late Mr B. T. Lowne informed me he had obtained a 25 % germination, at which figure the 'reproductive capacity' would be about 60. The average germination of *R. tripartitus* var. *terrestris* is perhaps about 60 % which would imply a similar 'reproductive capacity'.

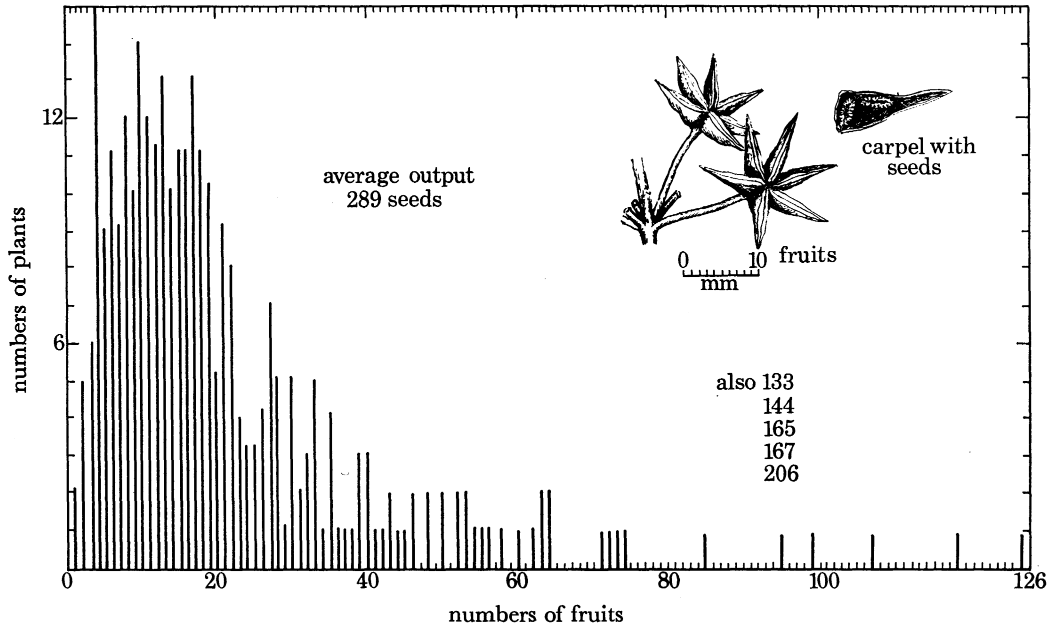

FIGURE 5. *Damasonium alisma*. Diagram showing frequency distribution of the numbers of fruits on 314 plants. Figures for five plants (beyond the range of the graph) are inserted. *Inset* are drawings of two fruits and also a dissected carpel showing the two contained seeds.

It is relevant to note that, in cultivation, *Ranunculus tripartitus* var. *terrestris* has been found to exhibit great susceptibility to 'damping-off' by fungal attack. A feature shared in an almost equal degree by *R. omiophyllus* and, from the statement in the *Flora of Gloucestershire* (p. 14), this would seem to be true also of *R. ophioglossifolius*. *R. hederaceus*, *Pulicaria vulgaris* and *Anagallis minima* appear to be rather less susceptible while *Myosurus minimus* and *Samolus valerandi* appear to be relatively immune.

It must be apparent that for some of the species enumerated in table 2 (e.g. *Chenopodium rubrum* or *Rumex palustris*) the offspring of only a few individuals could suffice to furnish many thousands of seedlings. However, the dense populations of these and other species which have appeared upon the mud floors of reservoirs and large ponds, when exposed by drought or drainage, are too large to be accounted for as the progeny of a few, hypothetically unobserved, marginal specimens. Successful germinations of fruits and seeds of these and other 'mud-species' that I have taken from mud as low down as 30 cm below the exposed mud-surface, has established that propagules of these species are present in a dormant condition and these germinate when exposed to light and air at suitable temperatures. It is probable that such propagules can remain viable for decades (cf. Salisbury 1921, p. 329), perhaps even for centuries. The multitudes of seedlings, of which a large proportion appear to be in the same stage of development, suggests, a quasi-simultaneous type of germination, under natural conditions, of these dormant propagules, a feature which is markedly exhibited in germination experiments carried out with freshly ripened seeds (see p. 230 *et seq.*) and which manifestly may be of great significance for survival in a habitat where the favourable conditions for germination are often of short duration.

When the mud is first exposed its high water content precludes any appreciable rise in temperature of the surface layers, but as these dry out and the effectiveness of the mud to conduct the heat of the sunshine away from the surface diminishes, the uppermost layers become warmed, the more so that the mud is often dark with humus, and with the access of air and escape of excess carbon dioxide, conditions for germination become favourable.

That seeds of the typical species may remain dormant for many years is evident from the frequent abundance of their seedlings upon exposed mud, of reservoirs and ponds, where previously regarded as rare, or unknown. The abundance of *Rumex palustris* on the mud of the Brent Reservoir in 1919 and of *Limosella aquatica* at Little Tring Reservoir in the same year, furnish examples. In the summer of 1935 the mud floor of Langmere, in Norfolk, presented abundant *R. maritimus*, many individuals about 60 cm high. The fruit production of an average sized plant was estimated, by weight, to be over 21800. *R. maritimus* was similarly abundant there some twenty years earlier, probably in the dry summer of 1911, together with a luxuriant growth of *Ranunculus sceleratus*, *Rorippa islandica* and *Myosoton aquatica* (cf. W. H. Burrell in Nicholson 1914, p. 29).

Purchas & Ley (1889, p. 250), writing of the occurrence of *Rumex maritimus* in Herefordshire, stated 'this plant is apparently only to be found for a year or two after large pools have been drained or dredged'. He comments also on the uncertain appearance of *Polygonum maculatum* (*nodosum*) 'though in some seasons in great abundance on dry pool beds (Purchas & Ley 1889, p. 254).

In 1921 a large pond in Buckinghamshire dried up for the first time in local memory and scattered over the mud floor were more than 60 plants of *Damasonium alisma*, some from the sides of deep cracks in the mud indicating that the dormant seeds had been covered by annual deposits of mud to a depth of 8 cm or more. Gross (1945) has recorded the abundance of *Alopecurus aequalis* and *Chenopodium rubrum* over acres of the sandy bed of Coate Water in 1944 'probably not previously uncovered in living memory'. In 1918 Carlton Rea (1919) recorded the very rare *Elatine hydropiper* 'in great abundance' on the floor of Westwood Poole near Droitwich and the astounding quantity of *Cyperus fuscus* observed by S. J. Coley near Cleveden in 1900, although previously unrecorded from the area (White 1912, p. 613). I have observed similar population surges of *Elatine hexandra*, and *Rorippa islandica*.

Very marked but less spectacular fluctuations are a feature, often commented upon, of the populations of *Radiola linoides*, *Anagallis minima* and *Cicendia filiformis*. Indeed this would appear to be a characteristic, shared in varying degrees by most, if not all, members of the mud flora.

The data furnished by the *Gloucestershire Flora* (Riddelsdell *et al.* 1948, p. 14) for the occurrence of *Ranunculus ophioglossifolius* in the same locality over a period of 31 years, records this species as present in 'great quantity' in eight of these seasons, but except in 1929 and 1930, these years of abundance were separated by intervals of from 2 to 7 years when there are stated to have been 'few or none'.

Propagules and dispersal

The propagules of these mud species are mostly very small (figure 6) and when freshly shed usually sink almost at once. In experiments on waterside species from this aspect Lloyd Praeger (1913) used dried seeds so as to ensure the greatest opportunity for flotation, but nevertheless found that the seeds of the following mud-species all sank within less than 1 minute: *Anagallis minima*, *Cicendia filiformis*, *Elatine hydropiper*, *Gnaphalium uliginosum*, *Limosella aquatica*, *Montia chondrosperma*, *Peplis portula*, *Radiola linoides* and *Samolus valerandi*. The achenes of *Ranunculus sceleratus* and *R. omiophyllus* floated for as long as $1\frac{1}{2}$ to $3\frac{1}{2}$ days but these are appreciably larger propagules (cf. figures 6, 18 and 19).

It would appear probable that all the small-seeded types and perhaps even the larger propagules, except the fruits of *Bidens*, are dispersed mainly on the feet of mud-frequenting birds. It should, however, be noted that Praeger agitated the fruits and seeds in water prior to his assessments of their behaviour, whereas in the natural habitat the ripe fruits or seeds could be

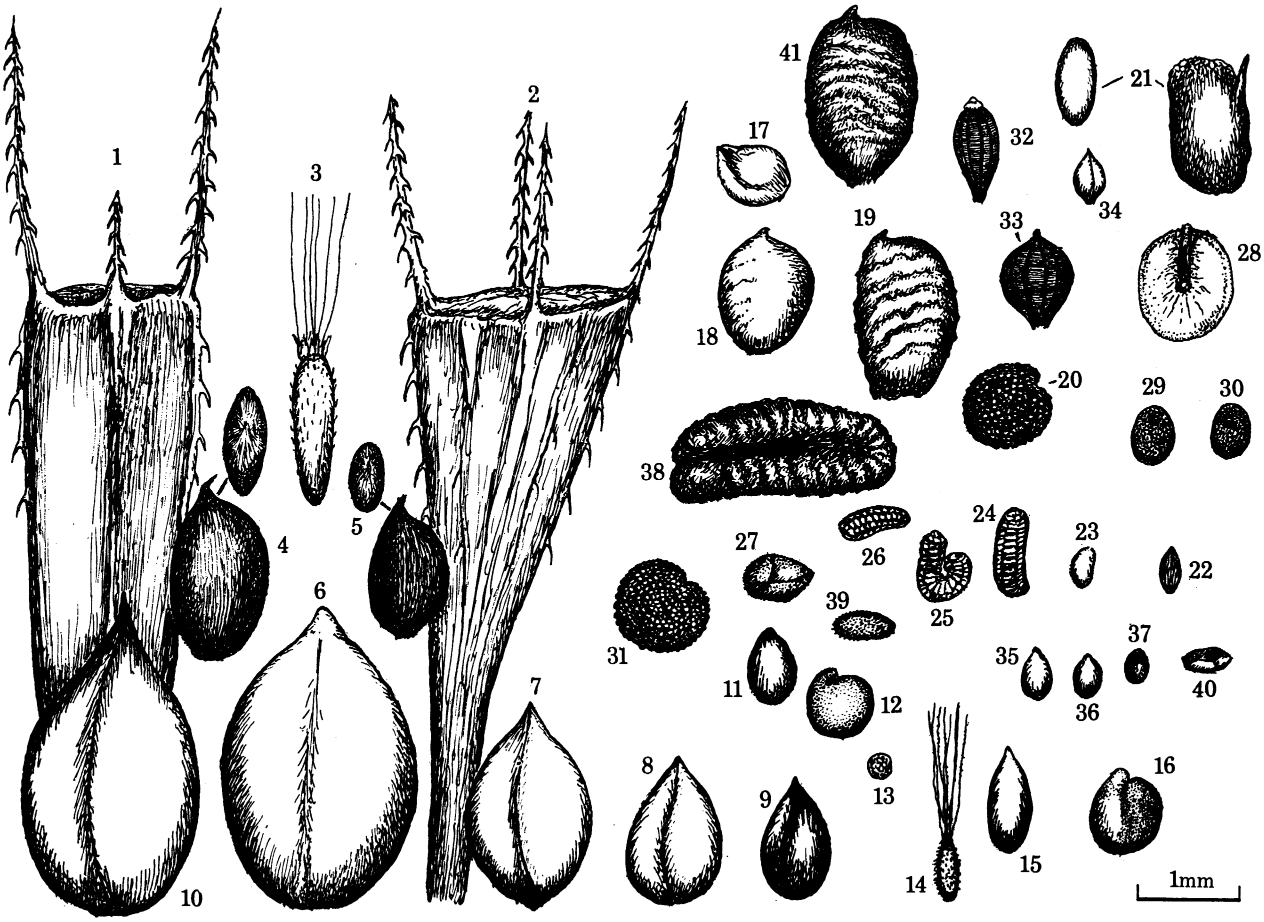

Figure 6. Propagules of 'mud-species'. All drawn to the same scale. 1, *Bidens tripartita;* 2, *B. cernua;* 3, *Pulicaria vulgaris;* 4, *Alopecurus geniculatus;* 5, *A. aequalis;* 6, *Polygonum nodosum;* 7, *P. minus;* 8, *Rumex palustris;* 9, *R. maritimus;* 10, *Polygonum hydropiper;* 11, *Peplis portula;* 12, *Chenopodium rubrum;* 13, *Cicendia filiformis;* 14, *Gnaphalium uliginosum;* 15, *Illecebrum verticillatum;* 16, *Rorippa islandica;* 17, *Lythrum hyssopifolia;* 18, *Ranunculus sceleratus;* 19, *R. hederaceus;* 20, *Montia chrondrosperma;* 21, *Myosurus minimus* (achene and seed); 22, *Crassula tillaea;* 23, *Radiola linoides;* 24, *Limosella aquatica;* 25, *Elatine hydropiper;* 26, *E. hexandra;* 27, *Anagallis minima;* 28, *Veronica scutellata;* 29, *V. anagallis-aquatica;* 30, *V. catenata;* 31, *Myosoton aquaticum;* 32, *Eleocharis acicularis;* 33, *Scirpus setaceus;* 34, *Cyperus fuscus;* 35, *Juncus bufonius;* 36, *J. mutabilis;* 37, *J. capitatus;* 38, *Damasonium alisma;* 39, *Drosera intermedia;* 40, *Samolus valerandi;* 41, *Ranunculus tripartitus* var. *terrestris*.

blown onto a water-surface adjacent to the exposed mud, in these circumstances the surface tension of the water would probably ensure their temporary flotation and thus water-carriage might be significant in relation to short-distance dispersal. Nevertheless, it is probable that adhesion to the feet or plumage of water-birds is the chief means of long-distance dispersal. In this context the following facts are of interest. *Crassula tillaea* is a species which was unkown in Hertfordshire but locally common in Breckland. During the last World War many reservoirs were drained to avoid their use on moonlight nights as guides to enemy aircraft. Marsworth Reservoir near Tring presented an area of exposed mud at this time and in 1941 during a hurried visit to observe the mud vegetation I observed a single fruiting specimen of *Crassula tillaea* on the mud towards the centre of the Reservoir. The area was well known as a resort of migrant birds and the war-time air activity near the east coast might be expected to augment the passsage from East Anglia westwards of mud-frequenting birds. That the species has, so far as I am aware, failed to persist in the area is a natural result of the restoration of the original water-level with the cessation of hostilities.

It is worthy of note that the propagules of several of the mud-species belonging to families without close affinity exhibit a similar type of sculptured surface with longitudinal ribs and cross bars, producing a scalariform surface (figure 6: 24, *Limosella aquatica;* 25, 26, *Elatine* spp.; 32, *Eleocharis acicularis;* 33, *Scirpus setaceus*). This may possibly indicate particular efficacy for the retention of a water-film that would facilitate adhesion.

When, after a period years, one, or more, of these species appears in large numbers on exposed mud, their origin from dormant propagules is most probable. However, the possibility of their re-introduction from the Continent, where they are mostly far more prevalent, must not be overlooked. The frequency of migrant birds, such as the Pochard and the Tufted Duck, from the south of Europe in the autumn, when these 'mud-species' are in fruit, emphasizes their possible importance in this role. The appearance of *Elatine hydropiper*, in 1935, at one spot on the 'Wildbrooks' in Sussex, although previously unrecorded for that County, may well be an example as also its recent appearance in West Scotland (Idle *et al.* 1970).

The largest propagules are the fruits of the species of *Bidens* which achieve efficient animal dispersal by means of the reflexed hooks by which they are beset so that their size and weight is no impediment. The comparatively large nutlets of *Polygonum nodosum* and *P. hydropiper* are buoyant and dispersed by water (cf. Ridley 1930, p. 224) as also by birds. The seeds of *Damasonium alisma* (figure 6; 38), which are remarkably large in comparison with those of other mud species, are not buoyant. Although at one time not uncommon, it appears to have always been very localized, and this may be an outcome of its low reproductive capacity combined with a dispersal that is not very efficient. The seeds are probably carried in mud but their size would militate against ready adhesion, although the rugose surface is retentive of moisture.

The internal carriage of seeds by birds as a means of dispersal is dependent for its efficacy upon the proportion that remain uninjured by the gizzard. That this proportion may be high was demonstrated by Guppy who obtained a 60 % viability of *Potamogeton* fruits that had been fed to ducks. These are ovoid about 3 to 4 mm in the longer axis. Vlaming & Proctor (1968) have shown that the propagules of a diversity of species can survive the passage through birds. They fed these to deerkiller birds and to ducks and determined the maximum times, between feeding and evacuation, when the droppings still yielded viable seeds. For *Rorippa nasturtium-aquaticum* this period was 4 h, for species of *Juncus* 17 to 27 h, while fruits of *Eleocharis* proved viable after a retention period of 120 h. They report flying speeds for the two species of over 50 miles per hour, so that effective dispersal by this means might extend to distances ranging from 200 to thousands of miles. The results with seeds of *Samolus pauciflorus* were negative and it may well be that the facets of these render them very susceptible to crushing by the gizzard action. It is however evident that the larger polished propagules of, for example, *Polygonum nodosum* may be significantly dispersed in this manner.

Of the species we have considered here, actual records of propagules that have been found in the mud upon bird's feet or feathers include the following: *Anagallis minima*, *Cyperus fuscus*, *Elatine hexandra*, *Eleocharis acicularis*, *Juncus bufonius*, *Limosella aquatica*, *Rorippa islandica*, *Samolus valerandi*, *Scirpus setaceus* and *Veronica anagallis-aquatica* [cf. Kerner (1904) and Ridley (1930)].

The grains of *Alopecurus aequalis* darken as they mature so that the spikelets become blackish in appearance. In this condition they are readily detached when shaken by a gust of wind. Eight hundred and forty such mature spikelets were shaken onto water in a white bowl so that their behaviour could be readily observed. Four days later, on 20 June, only nine spikelets had sunk and even after 10 days all but 22 (i.e. 2.6 %) were still floating upon the surface. As water replaced the air between the glumes the spikelets sank and after 10 days 15.5 % had done so. By this time, however, grains in some of the water-logged spikelets had germinated and their capacity to float was thereby maintained. It is thus apparent that for this species dispersal both by wind and by water may obtain. Moreover, the ripe grains are somewhat flattened, about 0.3 mm thick (cf. figure 6; 5) so that wet spikelets readily adhere to a surface with which they come in contact and long-distance dispersal on the feet and feathers of birds is probably frequent.

It should however be emphasized that even on still water about 60 % of the spikelets sink after 11 days and so come to rest upon the mud, while when subjected to wind turbulence they may sink much sooner, perhaps to remain dormant till again exposed by drought conditions.

Dry and mature spikelets of *A. aequalis* have an average weight of about 0.26 mg and the contained grains from 0.12 to 0.14 mg. The largest grains measured were 1.5 mm long by 0.75 mm broad and 0.32 mm thick, but grains measuring only 0.5 to 0.75 mm by 0.29 mm were found to be viable.

The number of fully developed grains in an infructescence, of which more than 100 were examined, ranged from 41 to 290. Ripe grains, as indicated by colour, may develop as early as mid-June and as late as October and it is to be noted that grains in the belated infructescences which are not dark brown but golden-yellow, nevertheless germinated freely. The average number of grains per infructescence, in a random sample of 100 was 154. Examination of 62 plants exhibited a range of from 1 to 27 infructescences with an average of 8 ± 0.5. The average output from these data would be 1240 ± 93 grains per plant. It is possible that the output of *A. aequalis* is normally larger than that of the perennial *A. geniculatus* in a single year, although the data available yield a difference that is not statistically significant. It must be noted that the grains of the perennial species are much larger and have an average weight that is rather more than double that of *A. aequalis*.

GERMINATION

Experiments on germination have been carried out on a large proportion of the species here treated and, except when necessary to elucidate particular aspects, the seeds employed were *freshly ripened* and normally sown within a few hours after collection. The germination behaviour of freshly shed seeds is obviously important although when, in a dry season, mud is exposed for a short period only, the seeds may mostly remain dormant till another dry season supervenes, when germination behaviour may be modified. A striking feature of the germination of these mud-plants is the influence on many of them of light and darkness. The reaction of propagules to illumination has been widely regarded as absolute, perhaps because those employed for experimentation have often been derived from a single plant or its offspring and not freshly shed. The results here reported reveal that propagules from different individuals of the same species can exhibit different responses to light and other environmental conditions and that the reaction may be one of degree rather than of kind. For these reasons the propagules employed for comparative studies have been freshly shed from the same individuals and, when many-seeded

TABLE 3. INFLUENCE OF LIGHT UPON THE GERMINATION OF SEEDS OR FRUITS OF 'MUD-SPECIES'

(Freshly ripened seeds or fruits of all species sown soon after collection except for those marked *)

species	observed germination in light (%)	observed germination in darkness (%) (except for brief inspection in dim light)
Alopecurus aequalis	73 to 100	up to 80 but more slowly
Alopecurus geniculatus	80 to 100	up to 100 but more slowly
Anagallis minima	38 to 82	rather less and slower than in light
Bidens cenua	up to 82	up to 80
B. tripartita	up to 100	up to 85
Chenopodium rubrum	84 to 100	0.09 to 7
Cicendia filiformis	?up to 22	0
Crassula tillaea	?87	?0
*Cyperus fuscus**	39 to 77	0 to 6
Drosera intermedia	up to 74	?0
Elatine hexandra	75 to 87	0.6 to 7.0
Gnaphalium uliginosum	up to 57	?0
Illecebrum verticillatum	?68	?0
Juncus bufonius	53 to 56	0 to 1.0
J. mutabilis (*pygmaeus*)*	44 to 62	?0
Limosella aquatica	72 to 96	0 to 6
Lythrum hyssopifolia	62 to 94	up to 28
Montia chrondrosperma	up to 58	?0
Myosoton aquaticum	up to 89	?0
Myosurus minimus	79 to 100	5.5 (but over 70% after brief exposure to sunlight)
Peplis portula	48 to 89	?0 to 1.1
Polygonum hydropiper	38 to 100	30 to 97
P. minus	26 to 84	12 to 30
P. nodosum	70 to 80	?59
Pulicaria vulgaris	86 to 100	34 to 93 (much more slowly)
Radiola linoides	up to 67	0
Ranunculus hederaceus	84 to 96	33 to 66.6 (more slowly)
R. sceleratus	34 to 98	0 to 3 (cf. E. Lehmann 1911)
R. tripartitus var. *terrestris*	43 to 97	up to 42 but more slowly
Rorippa islandica	73 to 98	0 to 66 (belated: mostly under 30)
Rumex maritimus	81 to 98	?
R. palustris (*limosus*)	86 to 100	48 to 95
Samolus valerandi	40 to 100	0 to 14
Scirpus setaceus	52 to 90	?0 to 14
Veronica anagallis	98 to 100	2 to 23 (49 in deep shade)
V. beccabunga	21 to 99	0 to 28
V. catenata	35 to 100 (usually over 80)	0 to 10.8 (very belated)
V. scutellata	20 to 58	?0

N.B. *A* ? preceding a figure indicates, merely, that the percentage is based upon one or two experiments only, *or* on seeds derived from but a single individual. Since experiments show that seeds from one individual may yield no seedlings in the absence of light whilst those from another may provide a small percentage, a '0' must not be taken to imply *invariable* absence of germination in darkness).

capsules were concerned, seeds were obtained from each capsule for subjection to contrasting conditions. Replicate sowings from particular individuals, employing large samples, behaved in most respects similarly. Only when small samples were alone available, from an individual plant, did the germination behaviour vary appreciably, as would naturally obtain if the apparent aberrations were in fact the extremes of a normal variation.

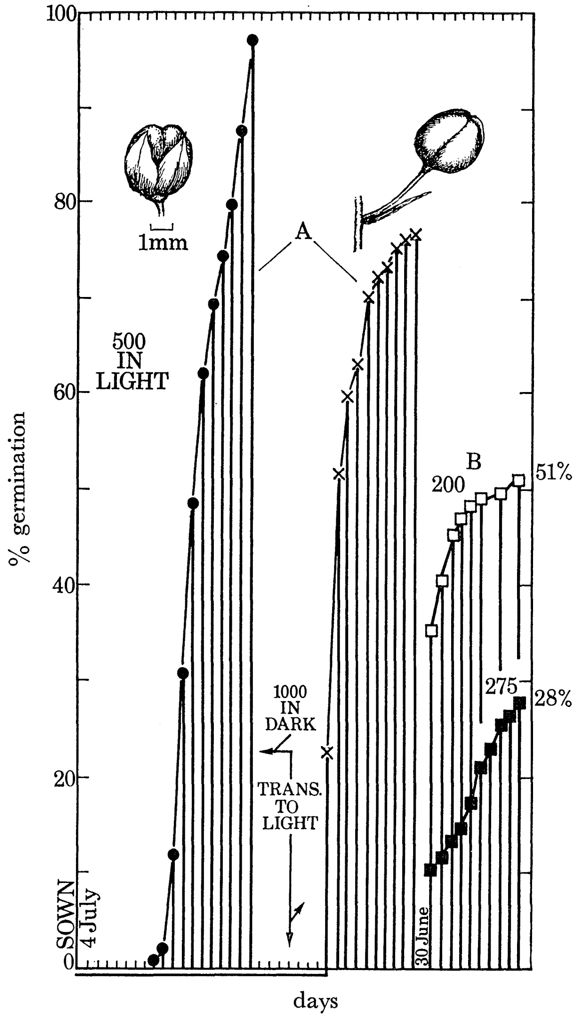

FIGURE 7. Germination of seeds of *Veronica beccabunga*. (A) Of 500 seeds sown 4 July and maintained in daylight. A, to right, 1000 seeds from the same plant, sown the same day and maintained in darkness for 22 days then transferred to light. (B) *Upper*, 200 seeds sown 30 June in light. *Lower*, 275 seeds from the same plant maintained in darkness. Ordinates represent percentage germinations. Abscissae, days from the first germination.

The germination of *Veronica beccabunga* in relation to light and darkness, though one of the less typical 'mud-species', affords points of considerable interest. Kinzel (1909) recorded 97 % germination in light but *no germination in darkness* for this species.

I sowed 1500 seeds from freshly dehisced capsules, all from the same plant, of which 1000 were maintained in darkness and the other 500 exposed to full daylight. These latter yielded 98 % seedlings after 10 days from the first germination (see figure 7*A*, on left). After the lapse of 26 days, since none of the seeds in the dark had exhibited any sign of germination, these were exposed to full daylight and within 4 days had germinated freely, attaining 77 % after 14 days in the light (figure 7*A*, on the right). Freshly ripened seeds from other plants, however, yielded varying low percentages of germination in the dark and an extreme example (figure 7*B*, right-hand graph) attained to 28 % germination in the dark, compared with nearly 50 % for seeds from the same capsules in the light. Since the cultures in the dark were examined daily, though very briefly, in subdued light to see if any germinations had occurred, it was possible that this short exposure to illumination might have brought about a response. Further batches of freshly ripened seeds were therefore sown and those in darkness were not examined until the controls, in light, had already yielded an appreciable germination. After a period of 15 days from the date of sowing 317 in the light had yielded 15.7 %, nevertheless the comparable number of seeds from the same capsules maintained in total darkness yielded 1.5 %. So while seeds of this species mostly fail to germinate in darkness, a small proportion of those of some individuals may do so.

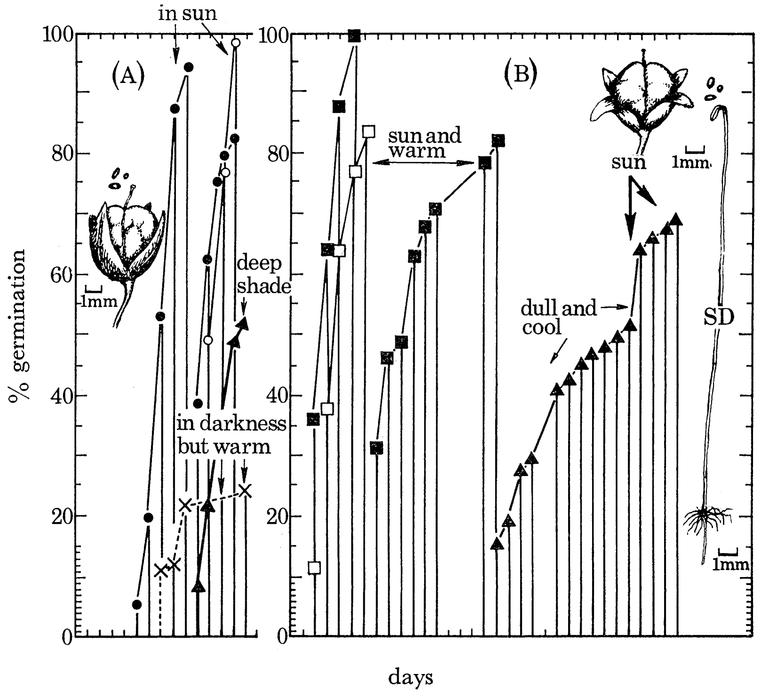

Figure 8. Germinations of seeds of (A) *Veronica anagallis-aquatica* and (B) *V. catenata*. The latter in full sunlight and in shade, the former in light, in deep-shade and in darkness. Ordinates represent percentages of the total numbers of seeds sown. Abscissae represent days from first germination. SD, etiolated seedling in dark. Scale marks on insets = 1 mm.

The most probable explanation of the results obtained is that the seeds contain an inhibitor that varies in amount in the individual seeds and is inactivated by light. Seeds which germinate in the dark may, it is suggested, contain little or no inhibitor. It is consistent with such an explanation that some of those seeds which do germinate in the dark may germinate almost as quickly as those in the light.

The rapidity of germination was also shown by the seeds of a small dark-blue-flowered strain of *V. beccabunga*. These ripened and were sown on 25 June. Nine days later over 65 % of the 500 sown had already germinated.

V. anagallis-aquatica behaves similarly. Kinzel reported that this species failed to germinate in darkness and I have little doubt this frequently obtains. The germination in light of *V. anagallis-aquatica* is presented in figure 8 from which it will be apparent that between 90 and 100 % can be attained within a period of from 3 to 5 days. Seeds from these same plants, sown at the same time, in darkness and subject to identical temperature fluctuations, yielded a minimum of 2 % and a maximum of 23 %, achieved within 8 days, subsequent to this no further germinations in darkness were to be observed.

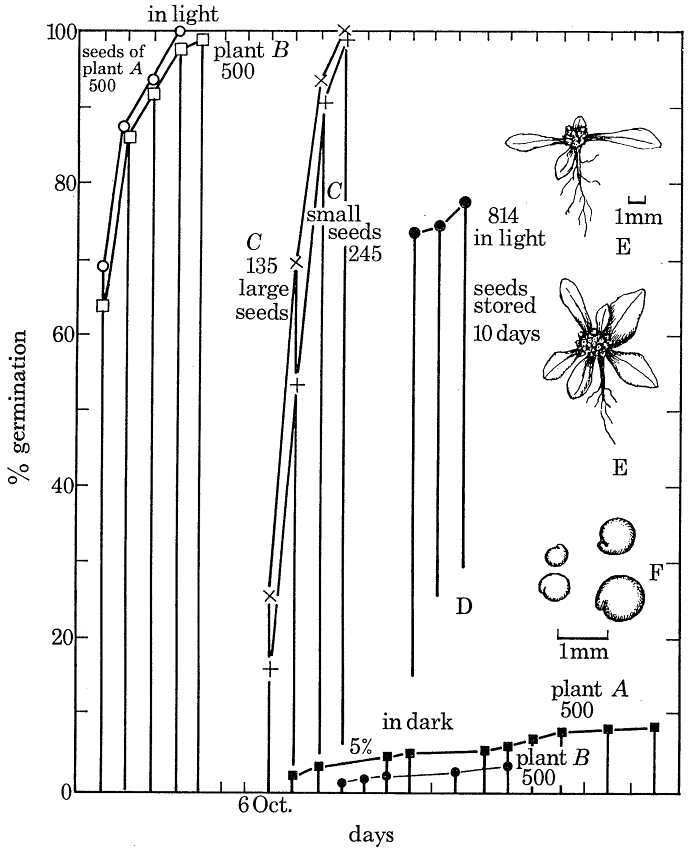

FIGURE 9. Germinations in light and in darkness of seeds of *Chenopodium rubrum* sown when freshly shed. (A) and (B), above and below, of 500 seeds of each plant in light and 500 seeds of each in darkness. (C) Germinations of 135 large seeds and 245 small seeds from the same plant. (D) On right, germination of 814 seeds stored dry for 10 days. Ordinates represent percentage germinations. Abscissae, days from first germination. E and E; Two autumnal short-day plants showing precocious fruiting; F., large and small seeds.

On the right of figure 8 there is portrayed the course of germination, in sunshine, of the seeds of three plants of *V. catenata*, these numbered 236, 370 and 510. They attained, respectively, 82 % in 10 days, 83 % in 5 days, and 100 % in 4 days. In the hot July of 1969, 330 seeds of a plant growing in a rather dry situation were ripe and sown on 19 July and 85 % had germinated within 1 week. Seeds of another plant sown in dull cool weather only attained to 50 % in 12 days but, with the advent of bright sunshine, the percentage germination rose to nearly 70 % during the next 4 days. In total darkness, under the same temperature conditions, the maximum germination recorded was 2 %. In one experiment, when 1148 freshly ripened seeds were sown, in autumn, and maintained in darkness the few germinations, mostly in spring, attained to 0.52 % in 193 days. After a long pause, further germinations occurred in late autumn, 412 to 421 days after sowing, bringing the total to 10.8 %. It would be rash to assume that higher percentages, *after a longer lapse of time*, might not occur, both with this and other species, in the dark. Two samples, each comprising half the freshly ripened seeds from five capsules of a depauperate plant of *V. catenata* were sown on 30 August. Germination began in 4 days and, 2 days later, the one had yielded 73 % and the other 76 %. The capsules of this plant contained an average of 44 seeds compared with 63 as the average content of capsules from well-developed plants. It is thus evident that, despite impoverishment and the consequently small seed output, the quasi-simultaneous germination was unimpaired and the percentage but little diminished.

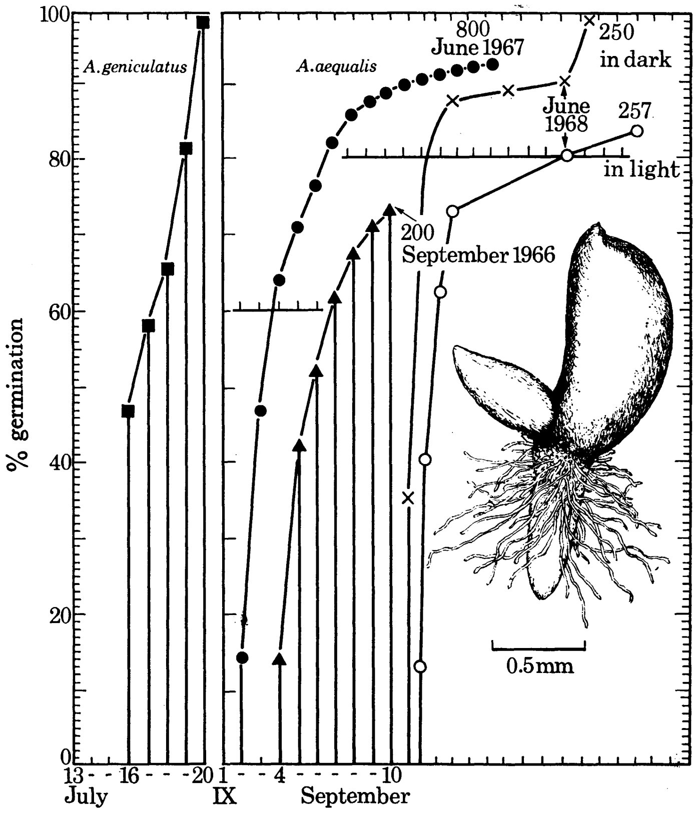

FIGURE 10. Germinations of *Alopecurus geniculatus* in light and of *A. aequalis* from three plants. On extreme right, the germinations of grains from the same individual, 250 in light and 257 in darkness, are represented. Ordinates, % germination; abscissae, days. Inset seedling of *A. aequalis* showing 'prop-hairs'.

One thousand seeds from each of two plants of *Chenopodium rubrum* were sown as soon as ripe. Five hundred from each plant being kept in the light and 500 from each plant maintained in darkness. In the light the course of germination for the seeds of both plants was essentially the same and yielded nearly 100 % within 5 days. In the dark, plant A yielded 8 % germination in 16 days and plant B 3 % in 8 days. However, although these sowings were, except with respect to the absence of light, maintained in favourable conditions for several months, no further germinations occurred (figure 9*A*, B).

The entire crop of seeds from a plant of *C. rubrum* normally presents large seeds and small seeds (figure 9F) but, as will be seen from the example represented (figure 9C), no significant difference in the total germination was observed, although, the larger seeds usually exhibit a slight tendency to germinate sooner than the smaller. Seeds of this species which were stored for 10 days in a dry state yielded over 70 % seedlings within 3 days from the first germination (figure 9D).

The spikelets of *Alopecurus aequalis* are normally shed intact when ripe, however, even when grains without the enveloping glumes are shed upon water they float. Of 167 grains removed from their glumes, all floated for 48 h, although by the third day 27 % had sunk. Six days after being shed 89 % had germinated and of these 39 % were still floating. It is to be noted that the intact spikelets sank as they became waterlogged and after the lapse of some days only exhibited a very small percentage germination compared with bare grains that had sunk. The relative percentages after a week were: intact spikelets 7 % and bare grains 90 %, which suggests that the presence of the glumes has an inhibiting effect upon germination. Six hundred of these intact spikelets which had sunk and failed to germinate were, therefore, carefully washed with several changes of water. Three days later no less than 20 % had already germinated and after another 3 days 360 more, bringing the total to 80 %, so that perhaps a water-soluble inhibitor from the glumes may be responsible for initiating the dormancy of the grains that sink into the mud. This may be the more important for survival since it was noted that grains deprived of their glumes which had sunk rose again to the surface after germination as the embryos developed.

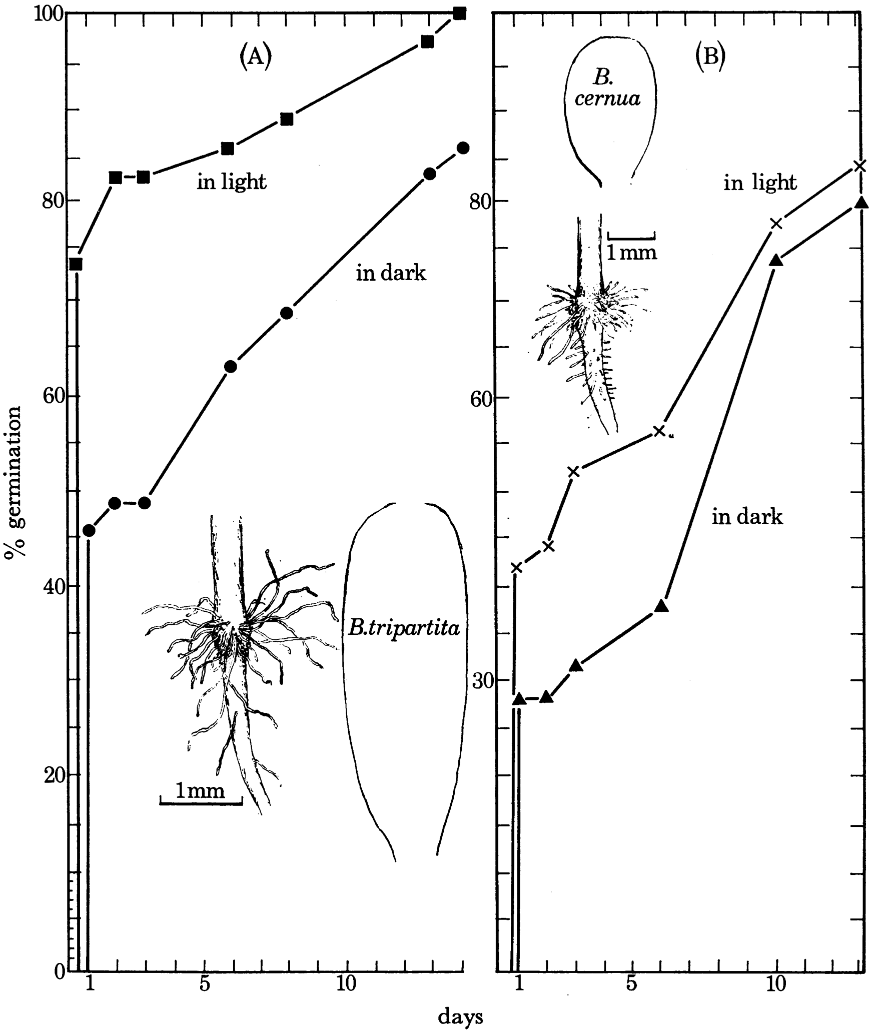

FIGURE 11. Germinations of *Bidens tripartita* and *B. cernua* in the light and in the dark. Inset, drawings of the cotyledons and collet region of the two species. The latter showing the 'prop hairs' arising from the swollen collet region.

That prolonged dormancy of *A. aequalis* grains may occur is manifest from the recorded abundance of this species over the mud floors of reservoirs, exposed by drought or drainage, after a period of years when it was absent or rare.

Of 800 grains of *A. aequalis* ripe and sown in June 1967, 93 % had germinated in the space of 15 days and over 80 % in the first six (figure 10). Two hundred grains from a plant, shed in September 1966, produced 73 % in 7 days. In June of 1968, 507 grains were collected from one plant and of these 257 were sown and maintained in darkness, the remaining 250 being sown in the light. These illuminated grains yielded 100 % seedlings in 11 days of which 88 % germinated within 4 days. The 257 grains, in the dark, started to germinate one day later attaining 74 % in 4 days and reaching a total of 85 % in 15. It is thus evident that light has but little influence on the germination of this species—a conclusion that appears justified for *A. geniculatus* also. This species can attain 100 % germination within 5 days (figure 10, left side) and like its congener achieves a high percentage germination in the dark although this takes place more slowly. The total germination of species of *Bidens* was found not to be greatly diminished by the absence of light, but the embryos of the fruits in darkness were slower to develop, although an appreciable proportion of the fruits began to germinate on the same day as those in the light (figure 11). On the collet of both species supporting root hairs were conspicuously developed (figure 11, insets).

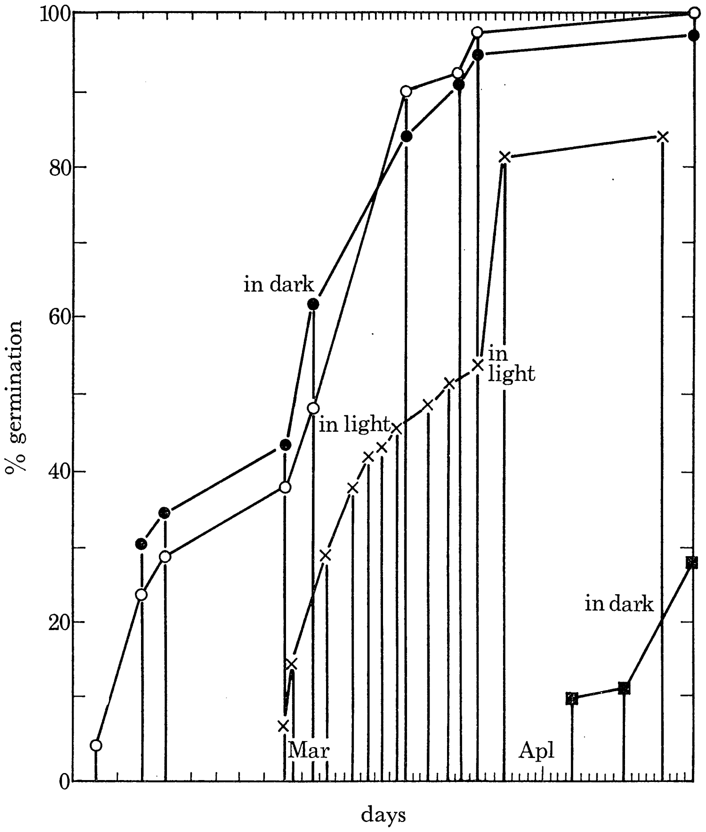

FIGURE 12. Germinations of fruits of *Polygonum hydropiper* (●, ○) and *Polygonum minus* (×, ■) in light and in darkness sown 5 September. Ordinates represent germination percentages on the same scale for both species. Abscissae, representing days from first germination, three times the scale for *P. hydropiper* as for *P. minus*. A period of 26 days is represented for the former and for the latter, 48 days in light and in the dark, 15 days of germination following an interval of 36 days after sowing.

It will be apparent from table 3 that of the 38 species, the germination of which has been experimentally studied, 23 yielded either no germination or but a small percentage in darkness. Of the other 15 species, 11 yielded an appreciable germination in the absence of light although far more slowly for most species than when illuminated. As a generalization, it can be asserted that germination of these 'mud-species' is normally slower in shade, and in total darkness usually meagre or even nil, but that the precise response is liable *to differ significantly between the propagules of different individuals.*

A quasi-simultaneous type of germination has previously been shown to characterise *Elatine hexandra* (Salisbury 1967*a*), *Limosella aquatica* (Salisbury 1967*b*) and *Pulicaria vulgaris* (Salisbury 1967*c*). Recently Timson (1965) has furnished valuable data respecting the germinations of *Polygonum hydropiper* and *P. minus*. He found that the fruits of the former would not germinate when stored dry but did so freely after they had been stored in water. I have obtained 90 % germination, within a fortnight, with *P. hydropiper* (figure 12) but its congener *P. minus* presented a marked contrast with germinations of the fruits from one plant which, from first to last, extended over a period of nearly forty days (figure 12). *P. minus* presents other interesting features. Whether the fruits be ripened and shed in late summer or early autumn they remain dormant till the following spring. Self-sown fruits have germinated rapidly in the second week in March of 1968, but in 1969 germination, though also rapid, occurred in April and in two flushes. The fruits of *P. minus* are of two types, trigonous and biconvex, the proportions of which vary greatly. One individual plant yielded only 0.8 % of trigonous fruits, whereas others yielded 32 % and an extreme example produced only 14 % of biconvex fruits. The trigonous

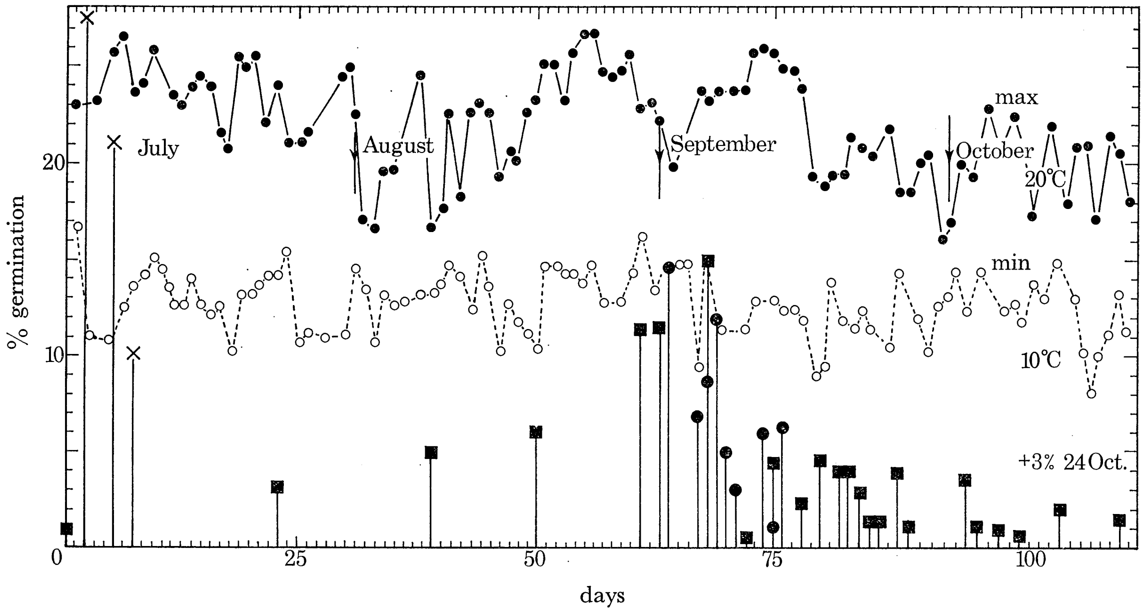

FIGURE 13. *Montia chrondrosperma.* Daily germinations of three sowings of freshly ripe seeds from different localities exhibiting markedly different rates. Environmental conditions including temperature fluctuations were the same for the most prolonged and most rapid except for the first 12 days prior to any germinations.

ripe and sown	totals
● 162, 16 May	63 % in 13 days
■ 233, 7 June	95 % in 115 days
× 47, 19 June	58 % in 6 days

fruits are in general larger and therefore probably tend to germinate sooner than the smaller biconvex fruits, a factor that may influence the pattern of germination behaviour (figure 12).

Other species to exhibit quasi-simultaneous germination are *Bidens cernua* and *B. tripartita* with 80% within from 4 to 9 days (figure 11).

Montia chrondrosperma (= *M. minor*) is a short-lived annual that flourishes during two separate seasons. A spring period that has its peak in April aand May producing ripe fruits in May and June, whilst a second crop flowers and fruits in the autumn. In figure 13 are shown the results of three sowings of seeds from spring fruits. From this it will be seen that the seeds from one plant, which yielded only a moderate total, nevertheless completed their germination within 6 days of the first appearance of a seedling. The seeds from several plants shed at the same time and sown at once on 7 June yielded 95% germination but occupied a period of no less than 115 days, whereas seeds from another plant also sown in June but derived from another

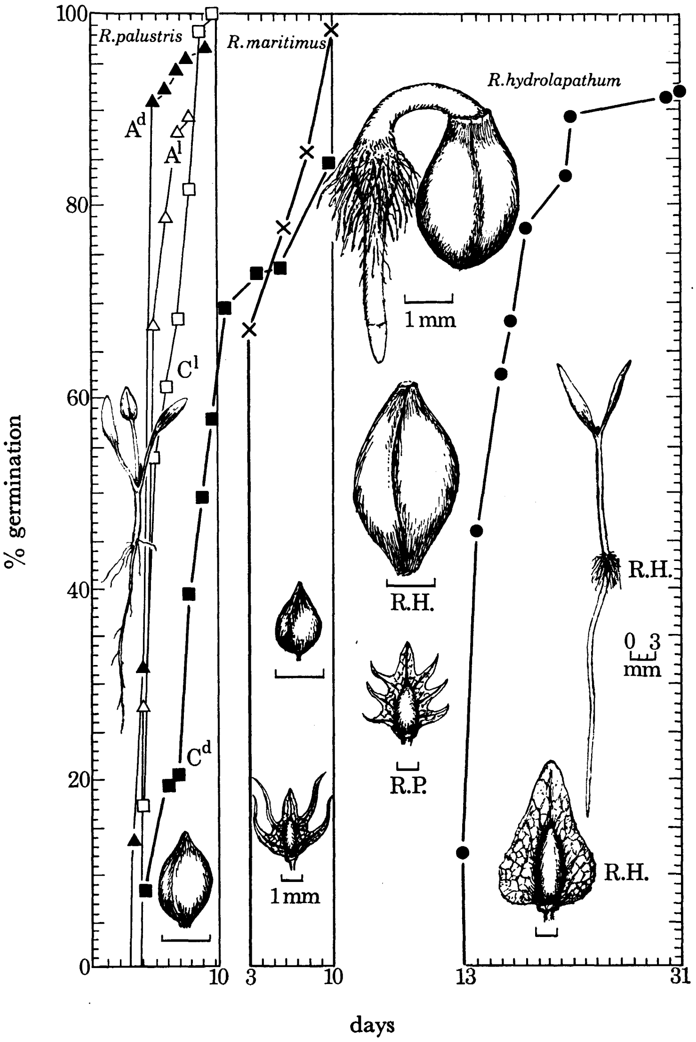

FIGURE 14. Germination of *Rumex* species. Ordinates represent percentage germinations on successive days. Abscissae represent days from date of sowing. Germination of *Rumex palustris* fruits from plant A, in light (A$^{\mathrm{l}}$), △ and in darkness (A$^{\mathrm{d}}$, ▲). Fruits from plant C in light (C$^{\mathrm{l}}$, □) and darkness (C$^{\mathrm{d}}$, ■). *R. maritimus* and *R. hydrolapathum* in light only. *Inset.* Drawings of fruits and perianth segments of all three species. Young seedling of *R. hydrolapathum* and much older seedling (R.H.). Scales = 1 mm unless marked otherwise.

locality occupied only 13 days. The maximum and minimum temperature fluctuations during these experiments are shown in figure 13 and since the periods of these germination experiments overlapped it will be manifest that the differences of behaviour cannot be attributed to varying temperature conditions.

The two docks characteristic of exposed muds, viz. *Rumex palustris* (= *limosus*) and *R. maritimus*, exhibit a germination behaviour that is quasi-simultaneous, over 90 % within a week.

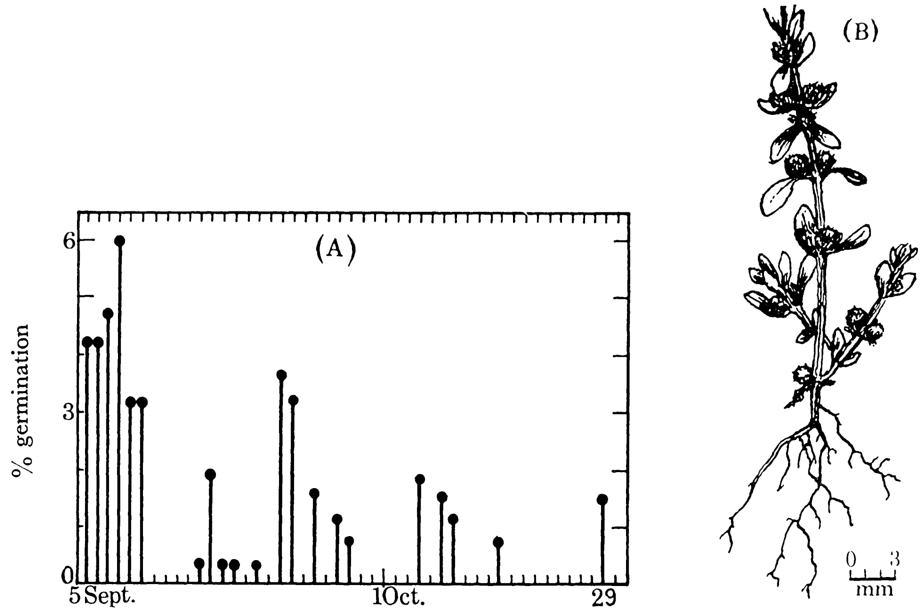

FIGURE 15. Germination of 270 seeds of *Peplis portula* sown 30 August showing (A) intermittent flushes with more than half the total germinating in the first 6 days. (B) An erect type.

In view of the specific name of the latter species it may be well to emphasize that about two-thirds of its recorded occurrences in this country are inland and not coastal locations. Furthermore, the comment that *R. maritimus* in Herefordshire 'is apparently only to be found for a year or two after large pools have been drained or dredged' and its abundance on the exposed muds of some of the Breckland Meres are pertinent reminders that this species is in no sense maritime although, like *Samolus valerandi*, it can tolerate soils with an appreciable concentration of soluble salts. On the alkaline peats of Somerset both species occur on exposed surfaces when the upper peat has been removed, doubtless from dormant fruits (Clark 1856).

Alike, in darkness and in light, the germination of *Rumex palustris* was found to be both high and rapid (figure 14). At normal temperatures the germination in darkness was somewhat slower, but the fruits of one plant maintained at higher temperatures (night min. 11.5 °C; daytime max. 22 °C) had, within a week, yielded a higher germination in the dark (95 %) than in the light (89 %). Subsequent culture of seedlings of plant C of *Rumex palustris* indicates, however, that these were of hybrid origin, *R. palustris* × *R. obtusifolius*.

The ripe fruits of *R. palustris*, when shaken up in water, sink, so they must normally be covered by silt before a drought brings exposure of the mud, with access to oxygen and consequent germination, facilitated by the dark colour of the mud in sunshine.

The germination of *R. hydrolapathum*—a species characteristic of a later stage in the plant succession on mud—is shown in figure 14 for comparison with its pioneer congeners. It should be mentioned that the fruits were freshly ripened; taken from plants growing by the Arun, on 8 October sown the same day and subjected to temperatures similar to those sustained by the other species. The more continuous character of the germination of *R. hydrolapathum*, occupying 18 days compared with only 6 or 7 days for the pioneer species, is sufficiently striking. Moreover, whilst for both *R. maritinus* and *R. palustris* germination began 3 to 4 days after sowing, 13 days elapsed before the first germination of *R. hydrolapathum*. Thus the statement in *The flora of the British Isles* (1962) (p. 554) that germination is in spring, would suggest that the interval between shedding of the fruits and germination is commonly far greater.

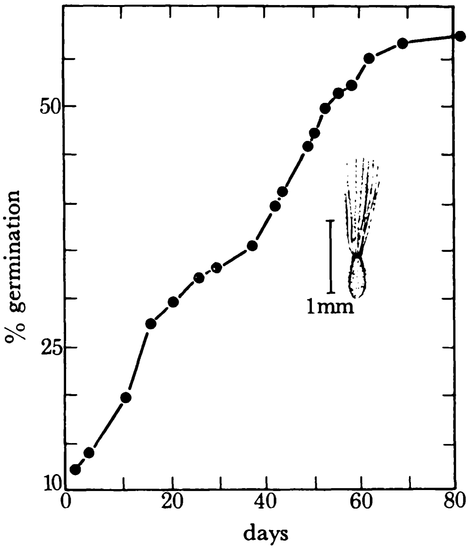

FIGURE 16

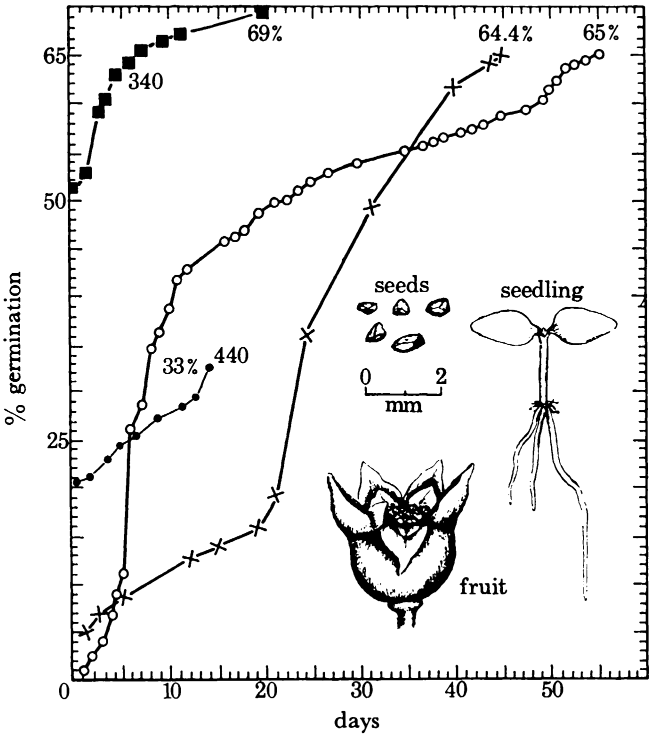

FIGURE 17

FIGURE 16. Germination of 3400 fruits of *Gnaphalium uliginosum* var. *pseudopilulare* showing emergence over a period of 11 weeks. Sown in autumn. First germination 4 March.

FIGURE 17. Germinations of *Samolus valerandi* seeds. 1050 ripe and sown on 31 July (○) and 1450 ripe and sown in September from another plant (×). Also seeds from the latter plant sown on 8 August 1968 one portion watered with fresh water (■) the other sowing with dilute sea water(●).

Contrasting with the quasi-simultaneous behaviour of most mud species, the seeds of *Peplis portula* germinated over a period of from 45 to 50 days but, as the behaviour of one plant's seeds illustrated in figure 15 shows, about half the germinations occurred during the first 6 days and subsequent germinations were mostly in flushes separated by intervals of 5 to 6 days. The germination of *Gnaphalium uliginosum* var. *pseudopilulare* was also prolonged. Three thousand four hundred fruits from a single plant germinated over a period of no less than 70 days in a continuous manner (figure 16). The prevailing habit of *Peplis portula* is prostrate but erect types also occur, one of which is illustrated (figure 15 (B)). It may be noted that the capsules of these erect plants contained an average of 19.4 seeds, compared with an average of 41.4 seeds for capsules from the prostrate type of plants growing nearby. The erect habit in this species appears to be rare but is not uncommonly exhibited by *Gnaphalium uliginosum*.

In their reaction to darkness the fruits of *Polygonum hydropiper* and *P. minus* presented a striking contrast in the samples tested. Whereas *P. hydropiper* may yield almost as high a percentage germination in darkness as in light, and no retardation, the fruits of *P. minus* not only yielded a much lower percentage in the dark but germination was markedly retarded (as presented in figure 12).

Sowings of *P. nodosum* indicated a, normally, high germination rate when well lighted. Fruits of only one plant were, however, tested for comparison of the effects of darkness. Ripe fruits were sown in early November and the first germinations did not appear till March, although, both in darkness and in light, on the same day. Yet though there thus appears to be no retardation, in respect to at least some of the fruits, the total germination in the dark was some 20 % lower than in the light.

Tests involving several thousands of seeds of *Samolus valerandi* (figure 17) harvested from plants growing in more than one locality would appear to indicate that, when exposed to light, the average percentage germination is usually about 65 % although sometimes not more than about 40 %. Without light no germinations occurred in most sowings. However, the seeds from one individual plant yielded a 14 % germination in darkness, a striking instance of individual behaviour.

Samolus valerandi, although occasionally found inland, is well known to be prevailingly coastal and can grow in soil containing over 12 % of sodium chloride. Tests were therefore made to study its germination on soil watered with rain water and on similar soil watered with dilute sea water. The latter yielded good germination but much more slowly. For instance during a period of five weeks after sowing the freshwater conditions yielded 40 % seedlings, but the brackish water conditions only 12.2 % in the same period.

From the graphs (figure 17) it will be seen that though germination can extend over a period of 45 to 55 days, some 40 % of the germinations occurred within a period of 3 weeks so that the trend towards quasi-simultaneous germination is quite appreciable.

The achenes of *Ranunculus sceleratus* mostly fail to germinate in darkness though a small proportion, perhaps not more than 3 %, may do so (cf. Lehmann 1911). In light the germination is high.

The three prostrate mud-species of *Ranunculus* present a marked contrast, since all exhibit a very appreciable germination in the dark. This difference may well be an important asset, having regard to the epinastic growth of the fruit stalks as the achenes ripen, a feature especially marked in *R. hederaceus*. As a consequence the fruits are often pushed down into the mud before the achenes are dispersed (cf. figure 13D, D). However, in these species germination in the dark is significantly slower than in the light, although both in light and in darkness germinations are spread over a similar period (figure 18B, B^1). Several sowings, each of between 150 and 200 achenes of *R. hederaceus* made on 13 and 14 June began to germinate in from 8 to 10 days. Those in the light yielded about 70 % within the first month. Alike, in darkness as in light, germinations in all tests extended over a period of about 70 to 80 days. But in darkness the major proportion of the germinations occurred within the last month, instead of the first weeks, although the achenes were obtained from the same individuals (figure 18).

The response to light of most of these 'mud-species' implies that germination will inevitably tend to occur when the habitats, through such circumstances as flood or drought, have been more or less freed from the shade of competitors. As a generalization it may be stated that, other factors apart, the larger the propagules of a species the less vulnerable it is to competition. It is therefore of interest to note that it is especially the 'mud-species' with relatively large propagules that exhibit the very marked germination in darkness.

Species with protracted germinations, as well as those in which this span is relatively brief, may, however, exhibit a marked tendency for a proportion of the propagules, sometimes a high proportion, to germinate within a few days of the first seedling appearing. For example, fruits of *Scirpus setaceus* shed in mid-October germinated over a period of 3 weeks, but when germination was initiated, 6 days after sowing nearly 27 % germination occurred within the next 4 days. Similarly, fruits of *Ranunculus tripartitus* var. *terrestris*, which only achieved their total germination after 3 weeks, attained 60 % of this total within 10 days (figure 4).

The self-sown fruits from a number of plants which were flowering and fruiting during August and September yielded numerous germinations from the beginning of September into early December. It must, however, be recognized that these seedlings present an aggregation of the germination behaviour of the fruits from a number of individuals and which were shed, when ripe, over periods of time that would often overlap but rarely, perhaps, be coincident. Hence

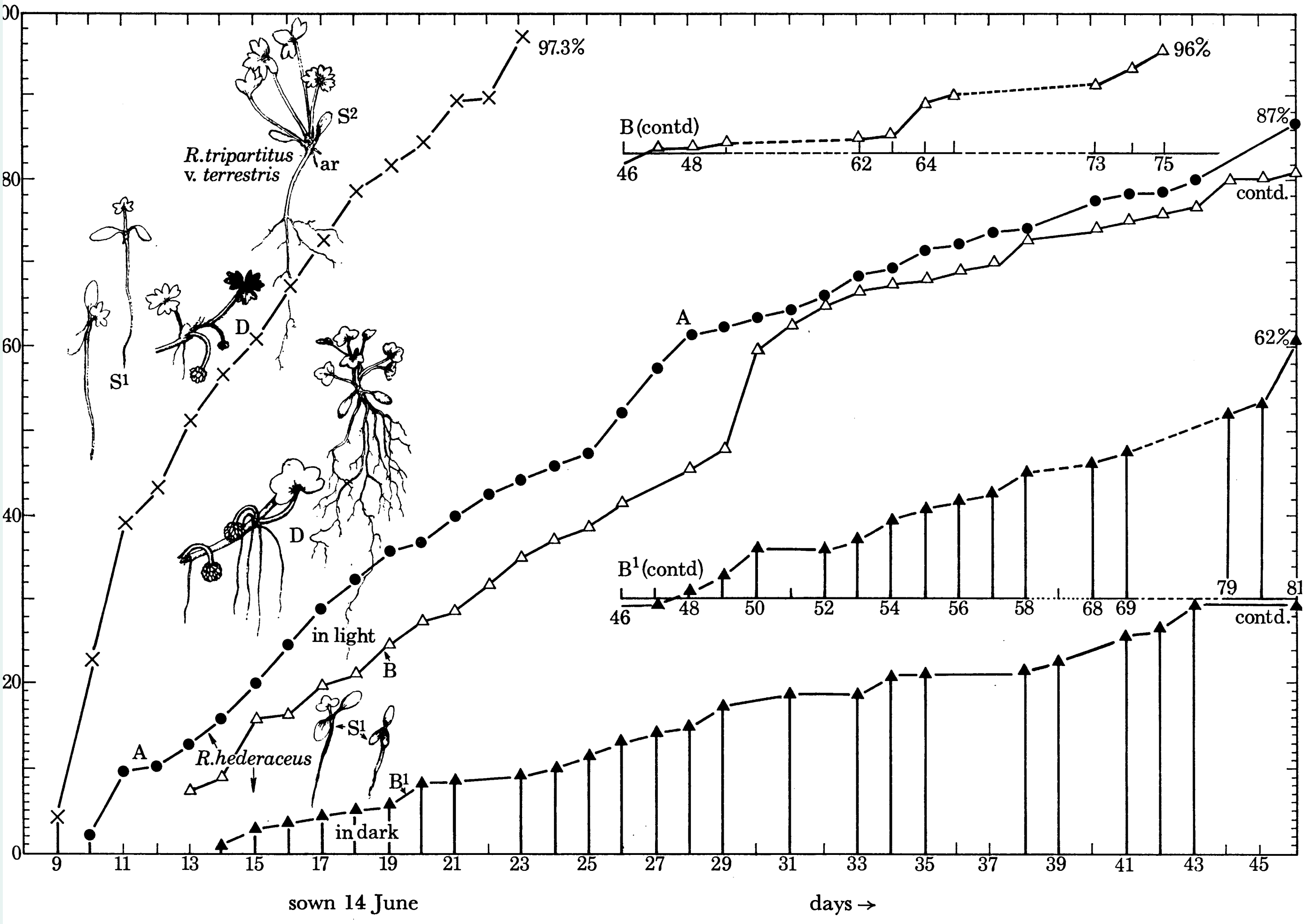

FIGURE 18. Germinations of June fruits of *Ranunculus tripartitus* var. *terrestris* (upper graph) and of *R. hederaceus* from Hampshire (A) and from Sussex both in light (B above) and in darkness (B¹ below). *Inset*, above, young seedlings of *R. tripartitus terrestris* (S¹) and an older seedling (S²) showing adventitious roots (ar) also mature fruits exhibiting epinastic curvature of fruit stalk (D). *Inset*, below, seedlings of *Ranunculus hederaceus* (S¹) of the younger tricotyledonous, and the mature fruit (D)

any quasi-simultaneous trend in the offspring of the individual becomes masked in the general seedling population.

Seeds of *Elatine hydropiper* were only available for a single test but half of these germinated within 10 days. At least twenty-two of the 'mud-species' exhibit quasi-simultaneous germination in a marked degree. But within the same species this trait is more marked with the seeds of some individuals than those of others.

The data furnished in the accompanying figures illustrating the quasi-simultaneous character of the germinations of many of these species are sufficiently striking. However, to avoid any possible bias, these have been presented as percentages of *the numbers of seeds sown*. Nevertheless if, as is not unlikely, the seeds which did not germinate can be regarded as non-viable, the quasi-simultaneous character of the germination could be significantly accentuated or be manifest when previously obscured. Thus, for example, *Ranunculus tripartitus* var. *terrestris* (figure 4) which yielded 37 % germination of the autumnal fruits sown, within the first 10 days, had in this period provided 77 % of the total that proved viable. Germination, under natural conditions, of all three white-flowered buttercups is perhaps prevailingly autumnal since numerous seedlings of the three species have been then observed. Spring germinations do also occur however, while in June seedlings may already have developed from fruits of the early spring flowers. For instance, ripe achenes of *R. tripartitus* var. *terrestris* which were shed on 25 May had already yielded 10 % germinations within thirteen days.

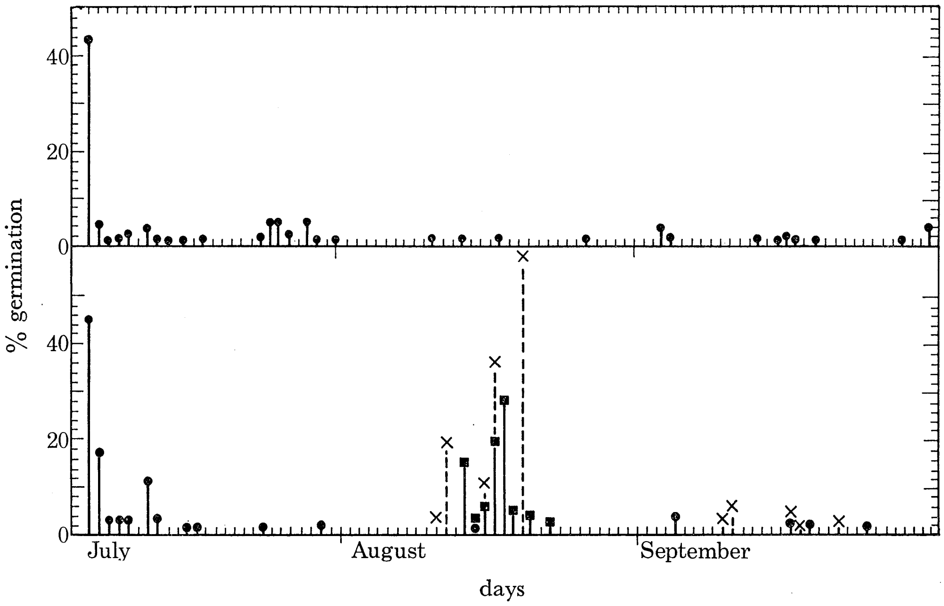

FIGURE 19. Germinations of seeds of *Rorippa islandica* from plants A to C exhibiting unusually protracted germination of a proportion of those sown. Plant A, germination total 76 % but 56 % in 7 days; plant B, germination total 89.6 % in 265 days but 85 % in 7 days. Plant C, germination total 98.4 % in 44 days but 92 % in 11 days.

● Plant A	483 seeds	56 % in 7 days	76 % in 271 days
× Plant B	228 seeds	85 % in 7 days	89.6 % in 265 days
■ Plant C	400 seeds	92 % in 11 days	98.4 % in 44 days

The germination of fruits of *R. tripartitus* var. *terrestris* which ripened and were sown in mid June is shown in figure 18 as also the germination of achenes of *R. hederaceus*, ripening at the same time, both in the light and in darkness. It will be apparent that the process in the latter species is both slower and more prolonged than with *R. tripartitus* var. *terrestris* whilst the percentage attained in the dark was appreciably higher. The June sowings of *R. tripartitus* var. *terrestris* were subject to an average night minimum of 14 °C (10.5 to 16 °C) and an average daytime maximum of 25 °C (17.2 to 31.6 °C). The autumnal sowings actually experienced a slightly higher average maximum (28 °C), but lower average minimum (13 °C), nevertheless the germinations in September occupied from 22 to 29 days compared with only 15 days from the first germination to the last in the June sowings, a difference that can perhaps be related to the difference in light-climate at the two seasons.

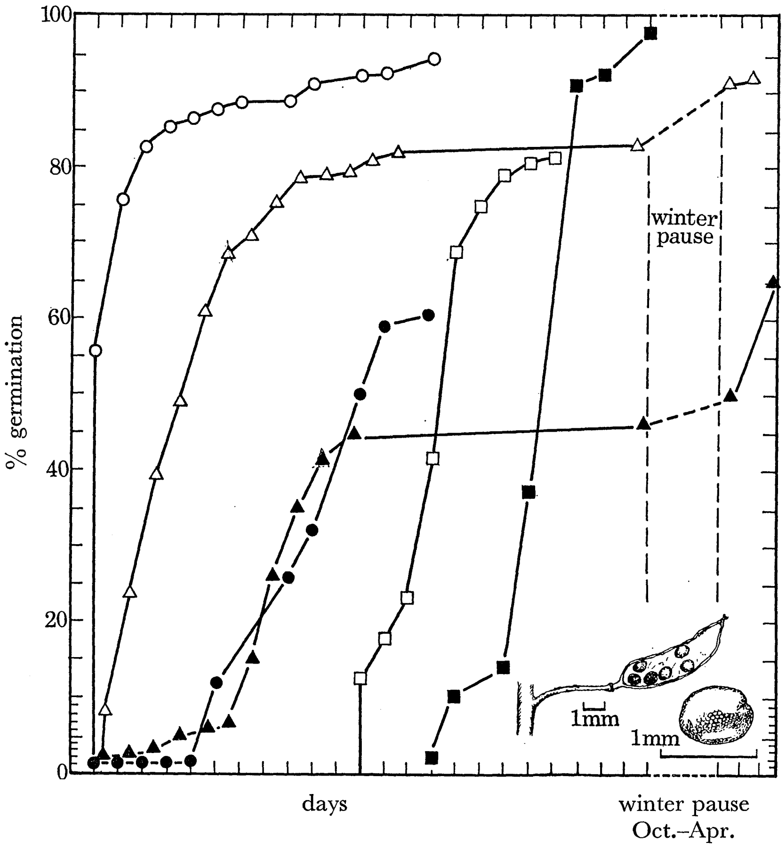

FIGURE 20. Germination of various sowings of *Rorippa islandica,* in light and in darkness. The broken lines (in the germination graphs for seeds sown in September) represent an interval from late October to April when no germinations occurred. Inset, drawings of a dehisced fruit, showing replum and unshed seeds, also a single seed five times larger.

D sown July {in light (○) in dark (●)}
E sown September {in light △ in dark ▲}
H¹ sown August in light (□)
H² sown August in dark (■)

Late autumnal fruits of *R. hederaceus* tested were slower to germinate than either the vernal or aestival samples. Achenes sown on 26 September only began germinating after 3 weeks and the maximum on any 1 day, namely 30.3 %, was on the fifty-eighth from the date of sowing the freshly ripened achenes.

The features of germination of *Rorippa islandica* merit special consideration from the point of view of individual variation. Seeds from most of the individuals tested yielded the quasi-simultaneous type of germination. Nevertheless, seeds from two individuals, that were ripe in

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June and sown immediately, both exhibited marked intermittence over a prolonged period (figures 19, 20).

The fruits of *Myosurus minimus* are normally shed in late June or July and remain dormant in the soil, usually covered by water later, till the mud is exposed and there is the vernal rise of temperature. Self-sown seedlings appeared in 1968 during the first week of January, on the soil of a pot, maintained in a moist condition but not immersed, where dead plants of *Myosurus* had been left undisturbed and placed in an unheated glass-house. Under similar conditions abundant seedlings appeared in the late December of 1969. Sowings in autumn that had been maintained in warmth failed to yield any germinations till mid-December, from which we may infer that the summer and autumn dormancy is an intrinsic characteristic which behaviour in warmer climes would also suggest.

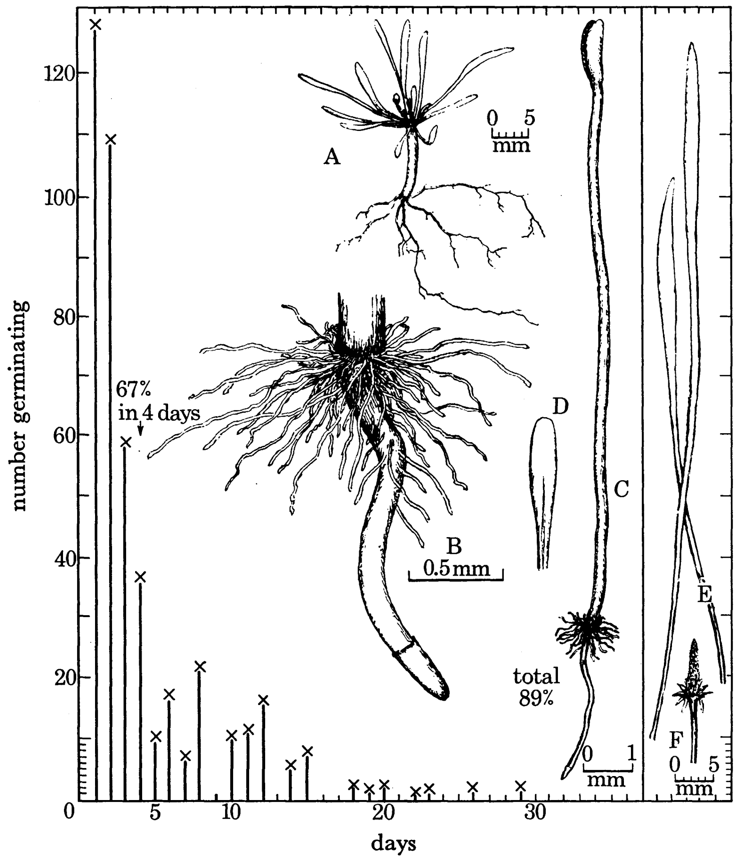

FIGURE 21. Germination of 500 achenes of *Myosurus minimus* showing 335 (67 %) in first 4 days. (A) Caulescent plant before flowering; (B) collet, bearing 'prop-hairs', of a 4-day seedling in light. (C) A 10-day-old seedling germinated and developed in darkness. (D) Cotyledon of seedling in light of the same age and on the same scale as C. (E) Mature leaves and flower on same scale as A.

The data presented in figure 21 show that almost 70 % of the fruits sown may have germinated within 4 days of the first appearance of a seedling. It will be noted also, from the drawing of a seedling grown in light (figure 21B), that the collet exhibits a well-developed skirt of 'prop-hairs'. *M. minimus*, with its low growth and small leaf-surface, is manifestly at a disadvantage in competition with many other annuals that could colonize similar bare areas. Its prevailing association with arable land where subject to winter inundation is significant. Cultivation ensures the open habitat whilst the aestival waterlogging precludes the germination of winter annuals, and indeed all competitors, until the fall of the water-table enables the soil temperature to rise adequately. It would hence seem probable that the quasi-simultaneous germination of *Myosurus* is the chief factor providing for its success in the struggle for adequate light and nutrients. Its natural habitat in Central Europe, where it is probably indigenous, would appear to be alluvium and the few occurrences recorded for England, in natural habitats, are consistent with this view.

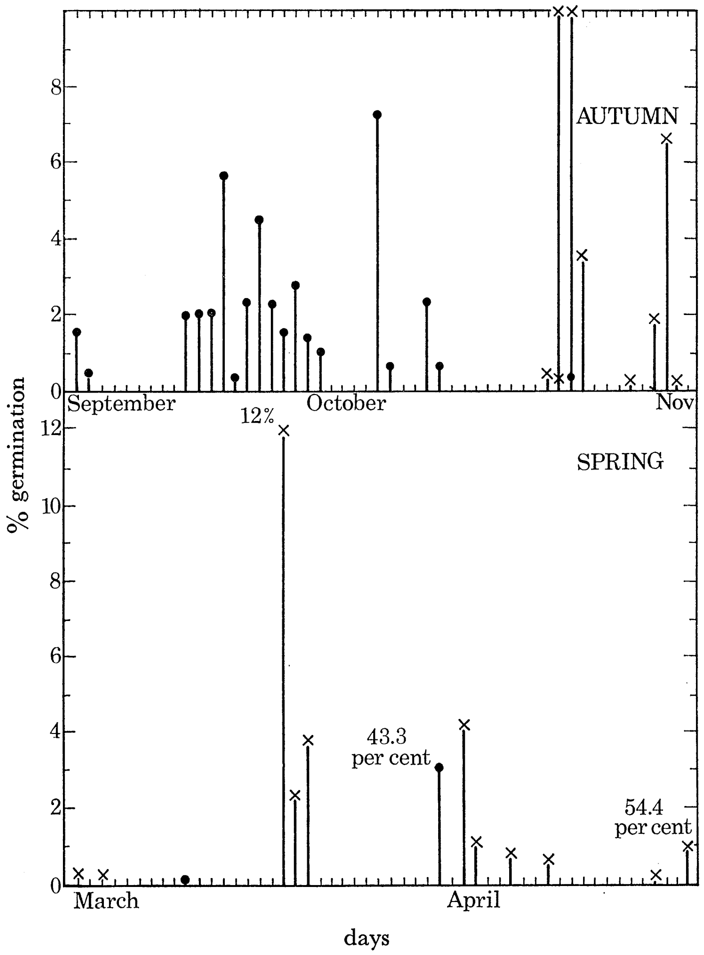

Figure 22. Germination graphs, of seeds of *Juncus bufonius* showing both autumnal and vernal flushes. Freshly ripened seeds sown on 20 July and 28 August.

● 465 seeds ripe and sown 20 July × 550 seeds ripe and sown 28 August

F. Nobbe and H. Hanlein sowed 400 seeds of *M. minimus* which yielded nearly 70 % within 8 days, but also *0.5 % after more than 3 years*. They also recorded a 1 % germination of *Veronica beccabunga* after nearly 3 years (cf. Crocker 1948, p. 42). Indeed, while a quasi-simultaneous germination for a high proportion of the seeds of these 'mud-species' is characteristic, a proportion exhibiting belated germination, or even prolonged dormancy, is not unusual. The flush of germinations for *V. catenata* in the dark, after an interval of nearly a year during which no germinations occurred, emphasizes the possibility that other species might have exhibited further germinations in darkness had the cultures been maintained for longer periods. In any event the delayed and often very belated germinations in the absence of light compared with the

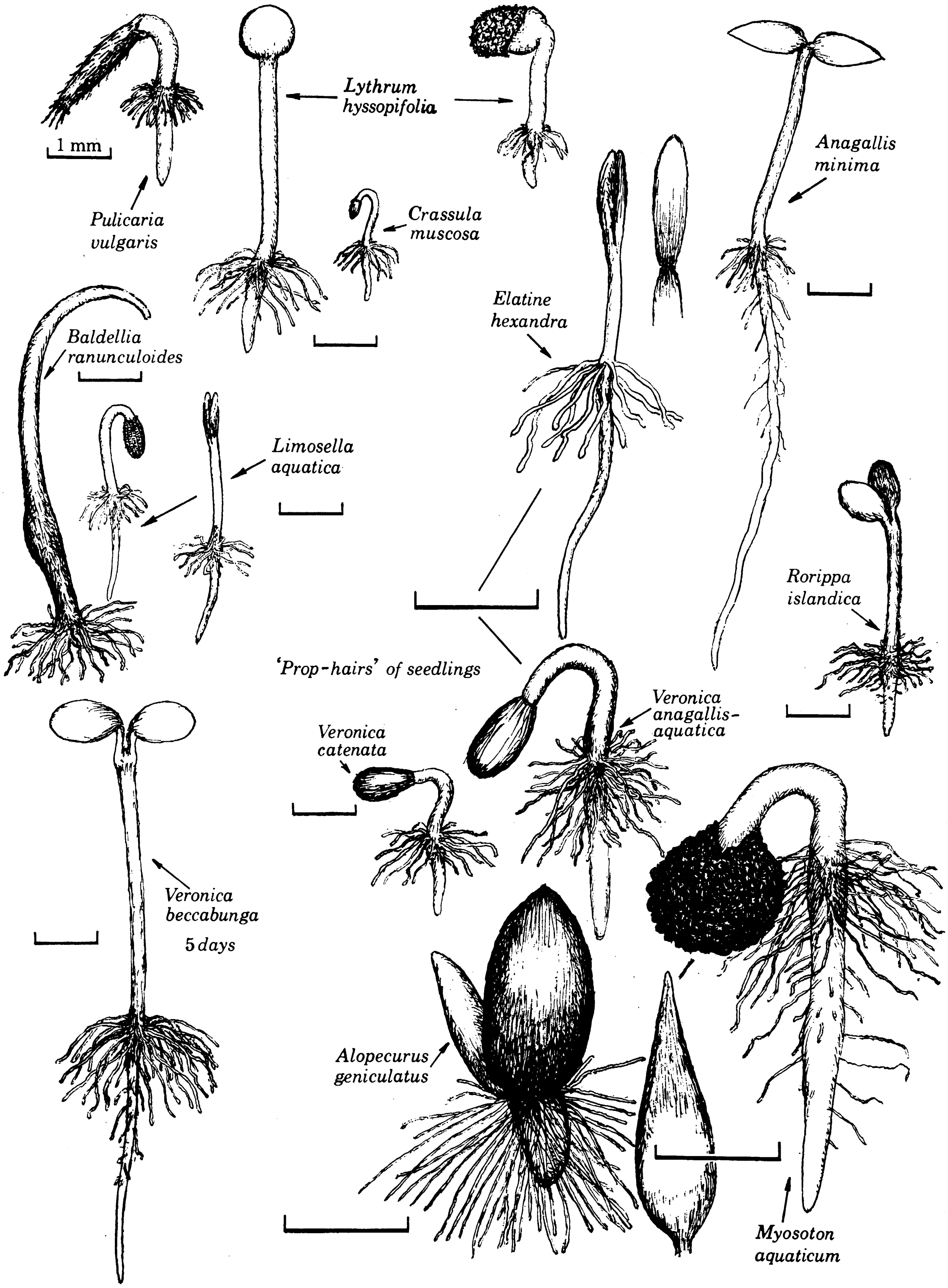

Figure 23. Seedlings of various species from mud, showing the 'prop-hairs' upon the collet. All scale lines = 1 mm.

quasi-simultaneous germinations in unshaded conditions suggests emphatically that, with the passage of time, some inhibitor in the seeds is inactivated gradually, whilst in the light this occurs very rapidly.

The development of root-hairs from the collet region of the germinating plant is a feature that produces anchorage and stability for the young seedling. For these 'mud-species' this is especially important when rainfall liquefies the exposed mud they have colonized. Most such are characterized by producing a skirt of numerous 'prop hairs' in this region. In figure 22 a number of examples are illustrated and in figure 24 a 2-day-old seedling of *V. catenata* is shown in which over 50 of these supporting root-hairs are seen arising from the collet region that is seen to be markedly thicker than the subtending axes, a feature that is frequently met with and

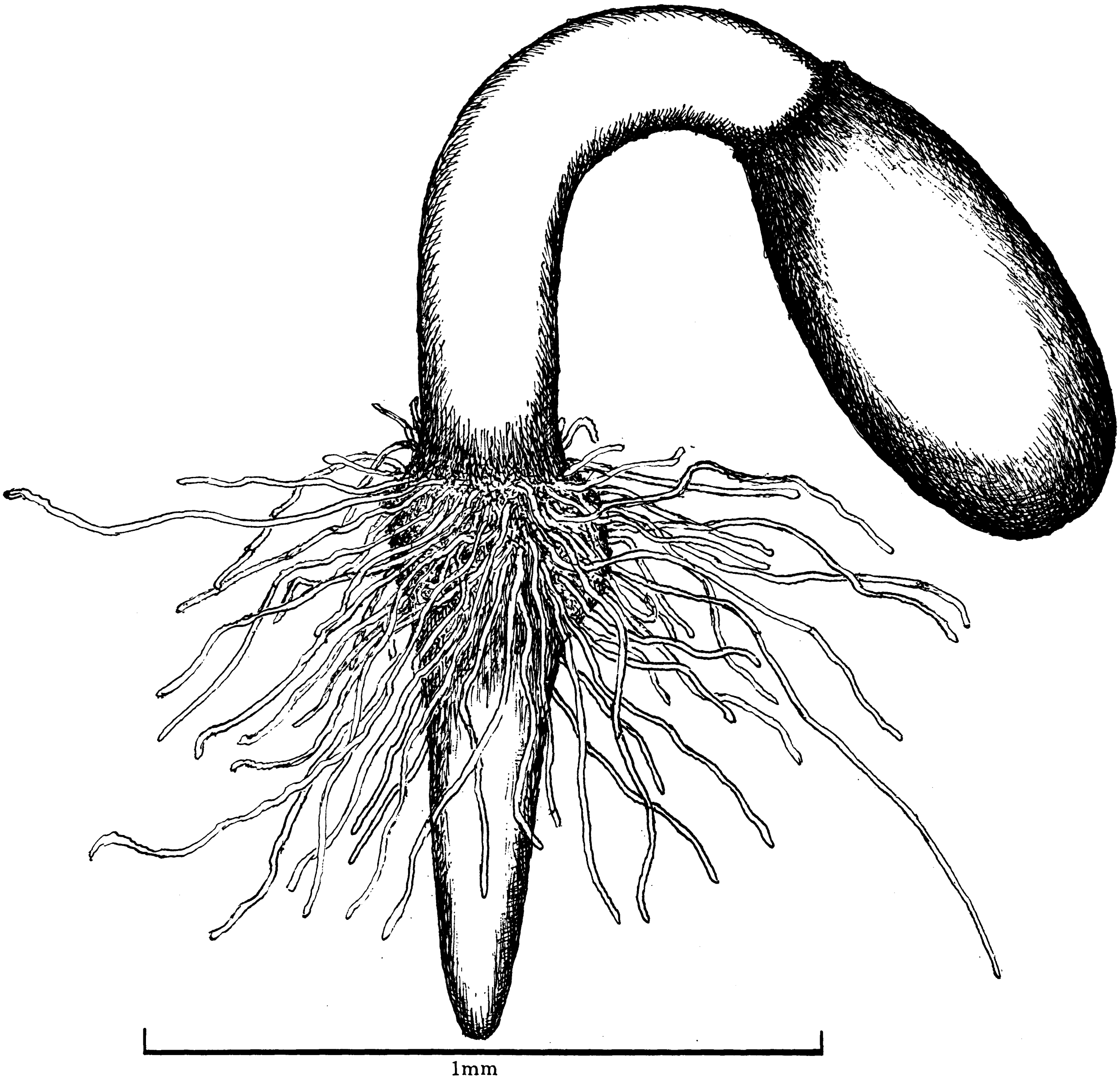

FIGURE 24. Two-day-old seedling of *Veronica catenata* showing the skirt of 'prop-hairs', over fifty, arising from the collet.

sometimes especially pronounced in seedlings of *Ranunculus omiophyllus*. The swollen collet region in the seedlings of *Bidens* is less pronounced (cf. figure 11) and here the 'prop-hairs' are also less conspicuous.

The seeds which have been observed germinating in the dark, naturally produce seedlings that are not only chlorotic but *aetiolated*. Such a 10-day-old seedling of *Myosurus minimus* is illustrated in figure 21C. This and other similar chlorotic seedlings had attained a height of 13 to 14 mm despite the very small food reserve which the seed of *Myosurus* provides (average wt. of a seed 0.03 mg). Such capacity for marked elongation may well be of significance for the species, so characteristic of situations subject to winter inundation, since germination might occur whilst a shallow layer of water still remains, although this would impose a check upon precocious rises of temperature.

An extended period of germination is normally a feature of several species and is particularly marked for *Juncus bufonius* (see figure 22). This rush, as also *Cicendia filiformis*, *Anagallis minima* and *Lythrum hyssopifolia* may all exhibit both autumnal and vernal germination of seeds shed at the same time and *Anagallis minima* and *Lythrum hyssopifolia* both exhibit a measure of seasonal dimorphism associated with this feature (see Salisbury 1969). In these two species seeds from some individuals may yield no autumnal germinations but for *J. bufonius* no tests have failed to yield seedlings at both periods, but individuality is marked by the very different proportions of the seeds from any one individual that germinate at these two periods.

It will be seen from figure 22 that the seeds from one plant of *J. bufonius* germinated mostly in the autumn with only about 5 % of the seeds germinating in the spring, whereas the seeds of the second plant represented, germinated almost equally in both spring and autumn. Seeds of another individual, ripe and sown on 17 June yielded only a few occasional germinations in the autumn, amounting in total to barely 10 %, of the seeds sown, and no further germinations occurred until the third week in March when a further 37 % germinated within 2 days. These facts sufficiently emphasize the striking differences in behaviour of seeds from different individuals and the polybiotic character of the seeds, both in this and other species, may have a high significance for persistence, or even survival, in this changing environment.

POLYBIOSIS

These studies of the behaviour of 'mud-species' have revealed that, as others have shown with respect to the plants of various habitats (e.g. Cavers & Harper 1966; Kruckeberg 1967) there are within the limits of, perhaps most, species, strains which differ in their biology.

The segregates to which we accord nomenclatorial recognition should, for practical reasons, be visually distinguishable. However, the physiological distinctions that are responsible for the biological segregates within any taxon would appear to be usually unaccompanied by distinguishable morphological concomitants. This is the more unfortunate since such biological strains, often only revealed by experimental culture, may have the greatest significance for occurrence and survival in a changing environment, whereas the morphologically distinguishable entities may not. The various strains, exhibiting marked restriction to, or preferential parasitism for, specific hosts, of the polybiotic *Orobanche minor*, for example, obviously differ physiologically. But strains that I have found restricted to, respectively, *Petroselinum segetum*, *Plantago coronopus* and *Cineraria maritima*, did not appear to present any morphological differentiation, although here the physiological differences are made manifest by field behaviour.

Polybiosis with respect to chemical distinctions may lead to selective animal attack, as with the cyanogenetic and acyanogenetic races of *Lotus corniculatus* (Jones 1962) or affect interspecific competition as with the root excretions of races of rice (Roy 1960).

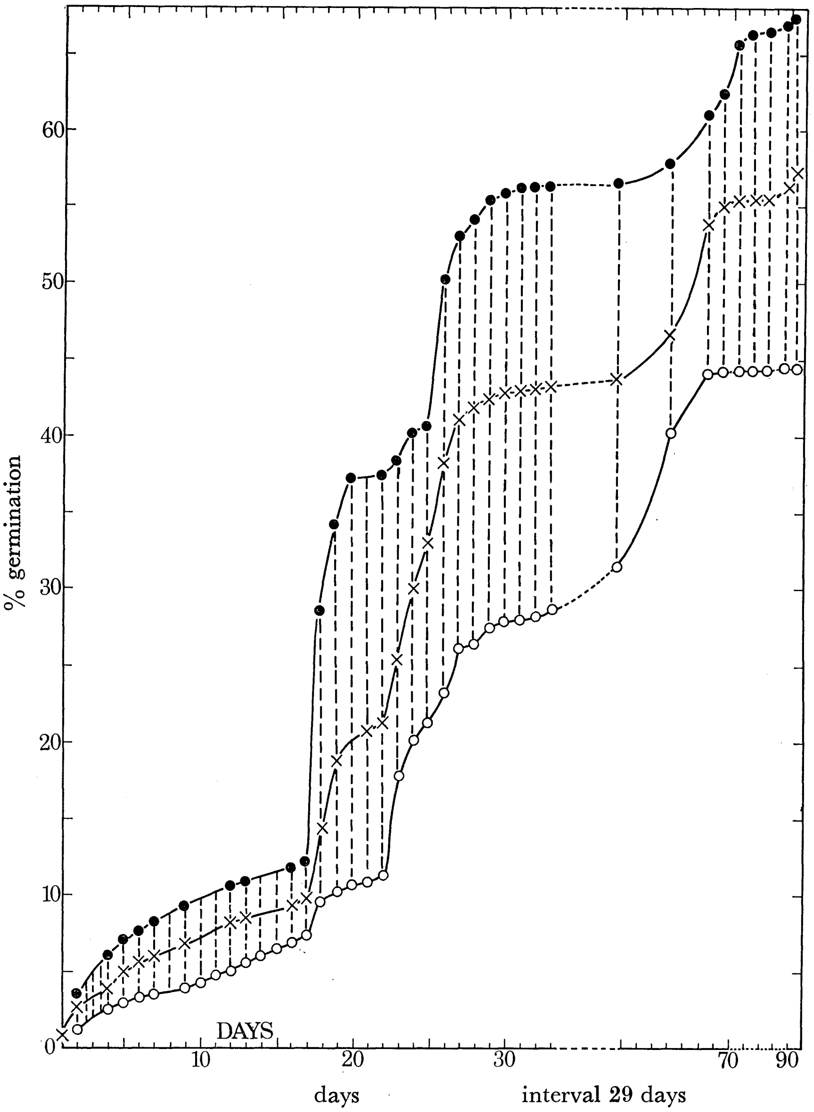

FIGURE 25. Germination of batches of seeds, stored for twenty-seven months, of *Veronica catenata* extending over a period of more than 70 days, showing throughout this period the maximum (●), minimum (○) and average (×) percentage germinations.

The persistence of such biological strains will obviously depend in considerable degree upon their genetic isolation. The prevalent self-compatibility and frequent cleistogamy of the 'mud-flora' species promotes this, whilst the role of efficient dispersal in bringing about spatial isolation is perhaps too often ignored in the emphasis upon its role in diminishing competition. Another type of isolation is well illustrated by a biological strain of *Caltha palustris* which the present writer experimented upon. Of a batch of *C. palustris* seedlings grown to maturity all but one flowered normally, toward the end of March or early April. The one exception flowered each year towards the end of February and *all its offspring shared this precosity*. The interval between the flowering of the early and the normal strain was amply sufficient to ensure the genetic isolation of the former.

LONGEVITY

The very large populations of a number of these mud-species that may appear on exposed mud, after many years of inundation, attests the longevity of their propagules under these conditions, although the precise span in years is speculative. It is pertinent to recall that in Dr Beal's experiments with buried seeds a 4 % germination of *Polygonum hydropiper* was recorded after 50 years (Crocker 1948, p. 37). With the object of obtaining evidence as to whether access of air and temperature fluctuations, from which propagules in mud are to a great extent protected, would appreciably reduce the percentage viability, freshly ripened seeds from 12 plants of *Veronica catenata*, which separately had been found to yield up to 85 and 100 % germination, were mixed together to achieve a more reliable average, and stored in an envelope in a shed subject to normal temperature fluctuations. After the lapse of 2 years and 3 months, samples of this mixed seed were sown separately in batches ranging in size from 280 seeds to 831. The average germination for all the random samples, representing a total of some 3000 seeds, was 57.4 %. A most interesting aspect of these tests, however, was that, despite the mixing, although most samples only departed from the average by from 0.3 to 2.3 %, the maximum was 9.7 % higher while the minimum was 13.8 % lower, thus emphasizing the polybiotic character of the component seeds which the mixing was inadequate to mask. So there is need for the utmost caution to avoid facile conclusions from average behaviour. Nevertheless, it is obvious from the data as shown in figure 25 which shows the course of average germination for all the samples as well as of the extremes, these conditions of storage account for a loss of viability that is probably about 44 %.

From these data it will be very obvious that experimental results, when the seeds employed for contrasting conditions *were not from one and the same individual*, are unreliable and may in fact be entirely misleading for wild species. Cultivated species, for obvious reasons, tend to be more uniform in character, so that published results relating to these are less likely to mislead, and indeed knowledge of the behaviour of mixed samples, normally available, is of practical importance.

A further aspect of interest is the protracted germination exhibited by these stored seeds, occupying over ninety days, for all samples, from the first appearance of plumules to the last germinations, thus presenting a notable contrast to the quasi-simultaneous germination, within 4 to 7 days, of the freshly shed seeds from these same plants. Since the proportion of seeds which normally germinate almost at once is about 45 to 55 %, it is possibly these which first lose their viability with storage when exposed to air.

Seeds of *Rorippa islandica*, similarly stored for 27 months, showed no indication of actual diminution since the germination totals ranged from 69 to 100 % similar to that observed with freshly ripened seeds from the same individuals. The stored seeds, however, occupied protracted periods of 70 to 86 days from the first to last germinations, whereas freshly shed seeds from most plants germinate within about a fortnight though, as already noted (cf. figures 19, 20), seeds of some individuals exhibit a protracted and intermittent germination, so the difference may be less significant than it appears. Seeds of other 'mud-species' stored for the same period, under like conditions, yielded very low germinations: *Pulicaria vulgaris*, 12.3 %; *Alopecurus geniculatus*, 3.5 %; *Elatine hexandra*, 5 %, followed by about 4 %, months later; *Lythrum hyssopifolia*, 1.3 %; and *Limosella aquatica*, 0.8 %. Nevertheless, these results do indicate a striking capacity to survive desiccation.

Fruits of *Rumex palustris*, taken from the mud of the Brent Reservoir from a depth of 30 cm, did not germinate when transferred direct to the surface of moist soil, but did so, freely, after drying in full sunshine. This suggests the need for fruit-coat rupture. However, propagules of other species taken direct from beneath mud have germinated without drying, as, for instance, *Chenopodium rubrum* and *Elatine hexandra*.

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Bold figures refer to the principal references.